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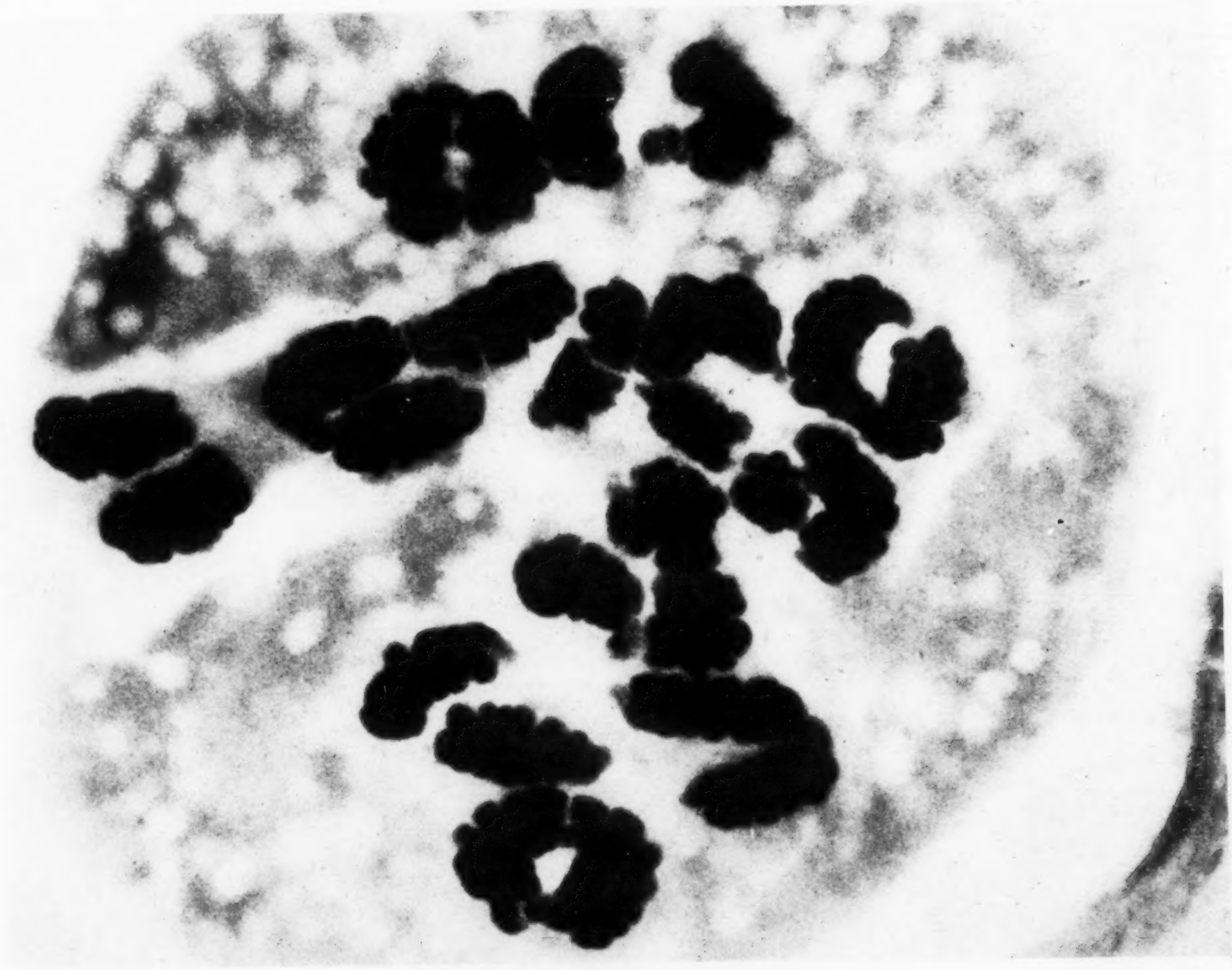

CHROMOSOMES AND CHROMOMERES
(See Page 371)

Cytoplasmic Inheritance **Alcohol and Eye-Defects**

An Age of Genius

AUGUST, 1927 VOL. 18, No. 8

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CONTENTS

CYTOPLASMIC INHERITANCE IN FLAX.....R. J. CHITTENDEN 337

ALCOHOL AND EYE DEFECTS.....F. B. HANSON and FLORENCE HEYS 345

"PERCENTAGE OF BLOOD" AND MENDELISM.....JAY L. LUSH 351

INHERITANCE OF ABNORMALITIES IN TEETH....A. M. CROSMAN 368

FORMS OF PLANT CHROMOSOMES.....JOHN BELLING 371

BRIEF REVIEWS AND COMMENTS

AN AGE OF GENIUS..... 343

BIOLOGICAL MIRACLES..... 367

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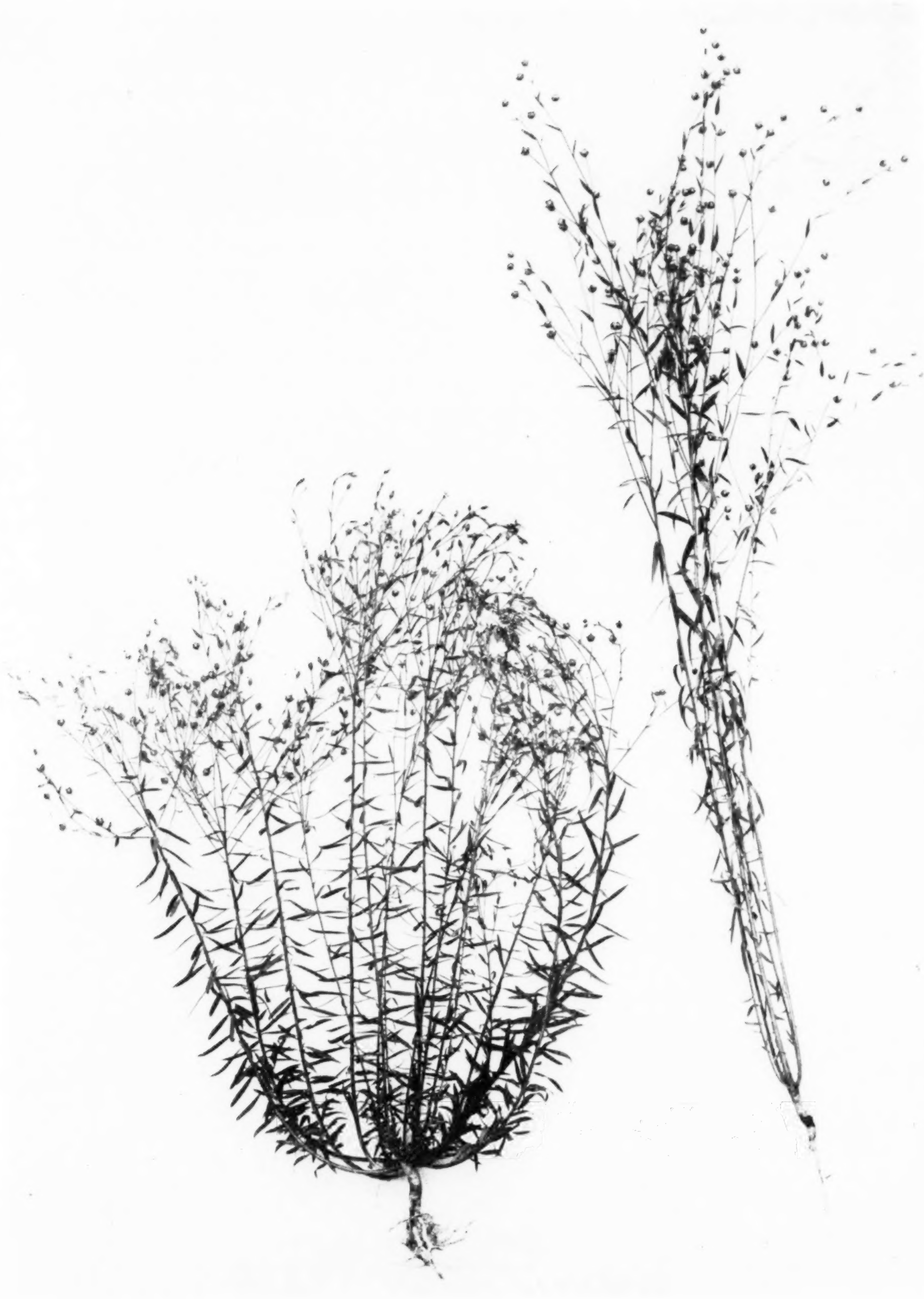


PROCUMBENT AND TALL FLAX

Frontispiece

On the left a plant of the Procumbent race of *Linum usitatissimum*, on the right a plant of the Tall race. The Procumbent form still has flowers and unopened flower-buds, whereas the Tall plant has finished flowering. The experiments indicate that some of the differences between these plants are not inherited through the chromosomes but through the surrounding protoplasm of the female cell.

CYTOPLASMIC INHERITANCE IN FLAX

R. J. CHITTENDEN

John Innes Horticultural Institution, Merton, England

THE rôle of the cytoplasm in the transmission of hereditary characters has been a much debated question. Amongst the more modern biologists the view of Loeb, that the cytoplasm is responsible for the transmission of the more important characters of the organism and on the rough outline thus provided by the cytoplasm the nucleus imprints the varietal differences, represents one extreme; that of Morgan* who maintains that "in a word the cytoplasm may be ignored genetically," represents the other. The mechanism of inheritance provided by the chromosomes, may be regarded as established beyond question. One type of extra-nuclear inheritance, plastid inheritance, first demonstrated by Baur, and now generally admitted, provides a second mechanism of inheritance, the individuality of the plastids being practically unquestioned.

The facts elicited from crosses between the Procumbent and Tall races of *Linum usitatissimum* by the work of Bateson and Gairdner provide definite evidence of the existence of a third mechanism of inheritance, and show that the cytoplasm as a whole, or some cytoplasmic constituent other than the plastids, possesses individuality. (There is evidence in material other than flax as yet unpublished to show that the cytoplasmic constituent responsible for the difference in the segregates of reciprocal crosses is not necessarily the plastids). Bateson and Gairdner's results were complicated by the fact that a peculiar abnormality, male-sterility, appeared in some of their crosses. Male-sterile plants have reduced petals and the anthers are more or less completely aborted. They appeared in the later generations of crosses between Procumbent (a peculiar plant whose origin is unknown) and the Tall fiber flaxes. The Procumbent form differs from the normal fiber flaxes in that it is procumbent in habit, branching much more from the base; the stems reach about two feet in length, lying at first flat on the ground, turning upward as the flowering begins, and finally standing more or less erect. The style is very pale in color, and the sepals shorter than is usual. It flowers about ten days later than ordinary flax. The Procumbent form is nevertheless like the Tall fiber flaxes evidently a variety of *Linum usitatissimum*.

Bateson and Gairdner's Results

The breeding results obtained by Bateson and Gairdner are shown in Table 1. The two male-sterile plants found in *C* are, they believe, probably due to self-fertilization of the male-sterile used. (Male-steriles occasionally produce a little pollen.) The one hermaphrodite in *D* is exceptional.

Bateson and Gairdner[1] showed then that male-sterility behaves as a simple Mendelian recessive to the normal hermaphrodite condition, and that it only appears in the cross of Procumbent by Tall, and not when the Tall is pollinated with Procumbent. They interpreted these results by assuming that the Tall forms, though they bred true on self-fertilization, were in reality heterozygous for male-sterility, a somatic segregation taking place before the formation of the eggs and pollen, so that the female side of the plant was pure hermaphrodite and the male side was pure for male-sterility. By means of this assumed phenomenon of anisogeny the Tall would breed true to hermaphroditism on self-fertilization,

*Amer. Nat. 60:491-1926.

MALE STERILE AND HERMAPHRODITE PLANTS

Figure 1

On the left of male-sterile plants, on the right a row of normal hermaphrodites. Notice the difference in the size of the flowers, and the fact that flowers of male-sterile plants do not open fully. Figures 1 and 2 courtesy of the *Journal of Genetics*.

though when used as a male on the male-sterile it would give only male-steriles. The Procumbent form was assumed to be pure for hermaphroditism. When Procumbent was used to pollinate a Tall, one would on this hypothesis expect nothing but hermaphrodites in F_1 and F_2. When the reciprocal cross was made, however, male-sterility would be brought in by the Tall pollen. Bateson and Gairdner assumed that in this case a normal segregation of male-sterility and its dominant normal allelomorph would take place in both the eggs and the pollen of the hybrid, so that in F_2 male steriles would thus appear in the ratio of 1 in 4.

Anisogeny not Supported by Recent Experiments

An alternative explanation was advanced by Chittenden and Pellew (1927), sowings being made to test its validity. Critical evidence would be provided by the following crosses:

(1) F_1 (ex Tall × Proc.) × Tall should give only hermaphrodites in F_1 and F_2
(2) Tall × F_1 (ex Tall × Proc.) should give only hermaphrodites in F_1 and F_2
(3) F_1 (ex Proc. × Tall) × Tall should give only 1 male-sterile: 1 hermaphrodite in F_1
(4) Tall × F_1 (ex Proc. × Tall) should give only hermaphrodites in F_1 and F_2
(5) F_1 (ex Tall × Proc.) × F_1 (ex Proc. × Tall) ..... should give only hermaphrodites in F_1 and F_2
(6) F_1 (ex Proc. × Tall) × F_1 (ex Tall × Proc.) ..... should give only 3 hermaphrodites: 1 male-sterile in F_1
(7) Male-sterile × F_1 (ex Tall × Proc.) ..... should give only 1 hermaphrodite: 1 male-sterile in F_1
(8) Male-sterile × F_2 (ex Tall × Proc.) ..... should give 3 results in F_1:
  (a) all male-sterile
  (b) 1 male-sterile: 1 hermaphrodite
  (c) all hermaphrodite

The results (as yet unpublished) of some of these are now available, and though incompatible with the old scheme based on somatic segregation at the formation of the ovules and pollen, are in harmony with that about to be described.

It is well known that the female parent contributes the whole, or the greater part, of the cytoplasm. And, as male-sterility only appears when there is cytoplasmic continuity from Procumbent, Miss Pellew and I suggested that this difference in the segregation from reciprocal crosses is due to a dissimilarity in the cytoplasms of Procumbent and Tall. Though the hermaphrodite gene* *P* from Procumbent

TABLE I—Breeding results obtained by Bateson and Gairdner in crosses involving procumbent and tall flax.

	Parents		F_1		F_2	
	Female parent	*Male parent*	Hermaphrodite	Male-Sterile	Hermaphrodite	Male-Sterile
A	Procumbent	× Tall	all	.....	361	109
B	Tall	× Procumbent	all	.....	716	.....
C	5 Male-steriles	× 3 Procumbents	101	2		
D	6 Male-steriles	× 6 Talls	1	640		
E	2 Male-steriles	× 2 sister hermaphrodites	14	12		
F	4 Male-steriles	× sister hermaphrodites	58	58		
G	1 Male-sterile	× a sister hermaphrodite	41	.....		
H	2 Hermaphrodites (F_2 ex A)	selfed	98	30		
I	5 Hermaphrodites ex E	selfed	378	140		
J	4 Hermaphrodites ex C	selfed	298	87		

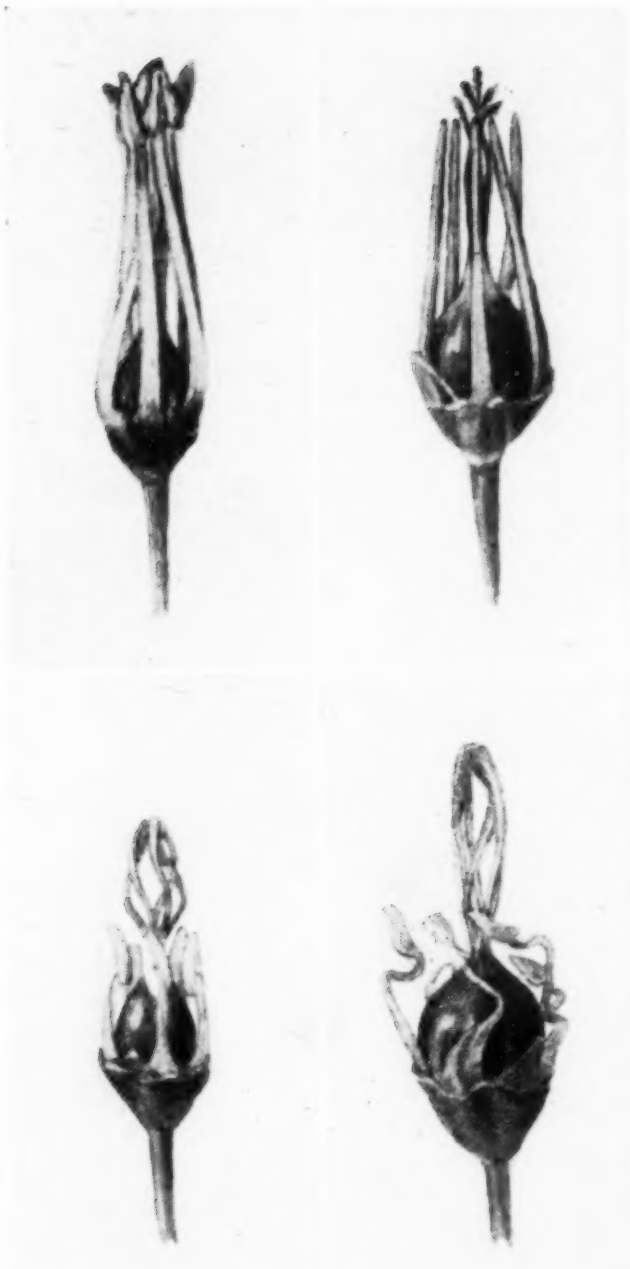
*These factors *T* and *P* here described as genes, since they behave as simple Mendelian units, may equally well be a block of genes or even a whole chromosome.

If *T* and *P* are whole chromosomes the partially male-fertile forms occasionally obtained may be due to an interchange of chromatin between the chromosomes T and P by means of crossing over.

MALE STERILE AND HERMAPHRODITE PLANTS

Figure 1

On the left of male-sterile plants, on the right a row of normal hermaphrodites. Notice the difference in the size of the flowers, and the fact that flowers of male-sterile plants do not open fully. Figures 1 and 2 courtesy of the Journal of Genetics.



NORMAL AND MALE STERILE FLOWERS

Figure 2

Hermaphrodite flowers at top, male sterile flowers below. At the left are shown the two types just before opening, at the right at a later stage, when the anthers of the hermaphrodite flowers have dropped. Note that those of the male sterile flowers shrivel but persist.

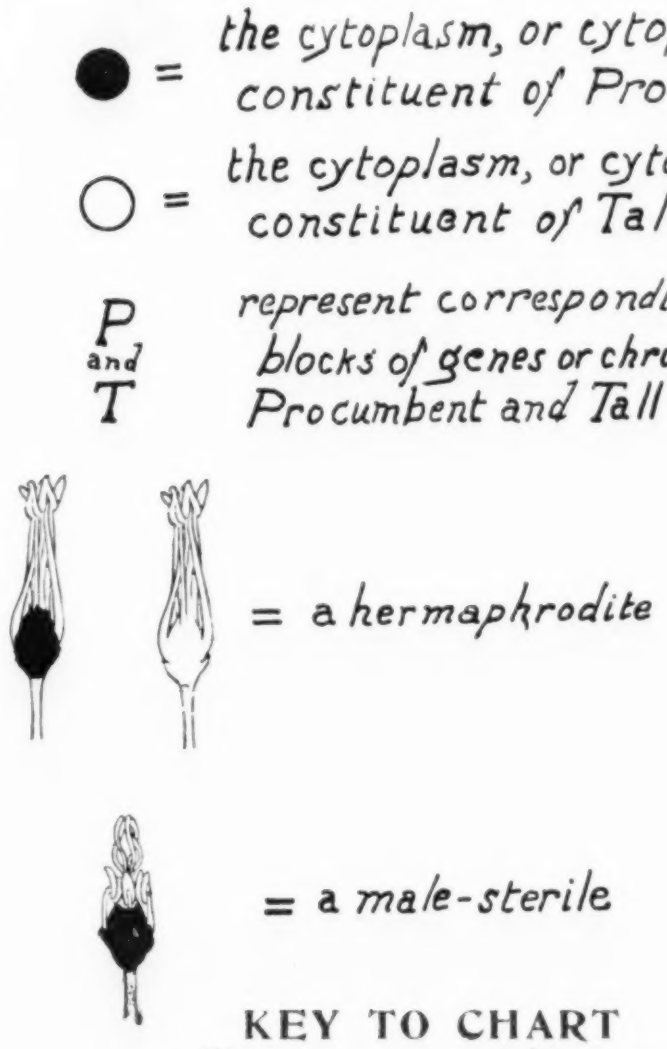
reacts normally in both cytoplasms, the corresponding gene *T* from the Tall when homozygous in Procumbent cytoplasm gives rise to male-steriles.

We have shown then that the appearance of male-sterility in one of the F_2's between Tall and Procumbent is due to a difference both between the cytoplasms and the genes of the Tall and Procumbent races; that this difference so affects the action of the gene *T* from the Tall race that when homozygous in Procumbent cytoplasm it gives a male-sterile plant.

Since the action of the gene *T* is affected it is peculiar that the gene *P* from Procumbent gives a normal hermaphrodite reaction in both cytoplasms despite their dissimilarity. Secondly, we might expect that, if the cytoplasm of Procumbent is sufficiently different from that of the Tall race to change the phenotypic expression of the gene *T* from Tall, it should have an equally disturbing effect on the expression of all the other Tall genes. This, however, is not the case, the segregation of flower color being similar in the reciprocal F_2's. The modern view is that each simple Mendelian character is not the direct result of the action of one gene, but is due to the mass action of the whole of the chromosome complement, on the end result of which one gene has a decisive effect. If this conception of the gene be accepted we find that in these crosses the action of all the genes is affected in one respect; that of hermaphroditism, while in other respects their action is apparently unchanged.

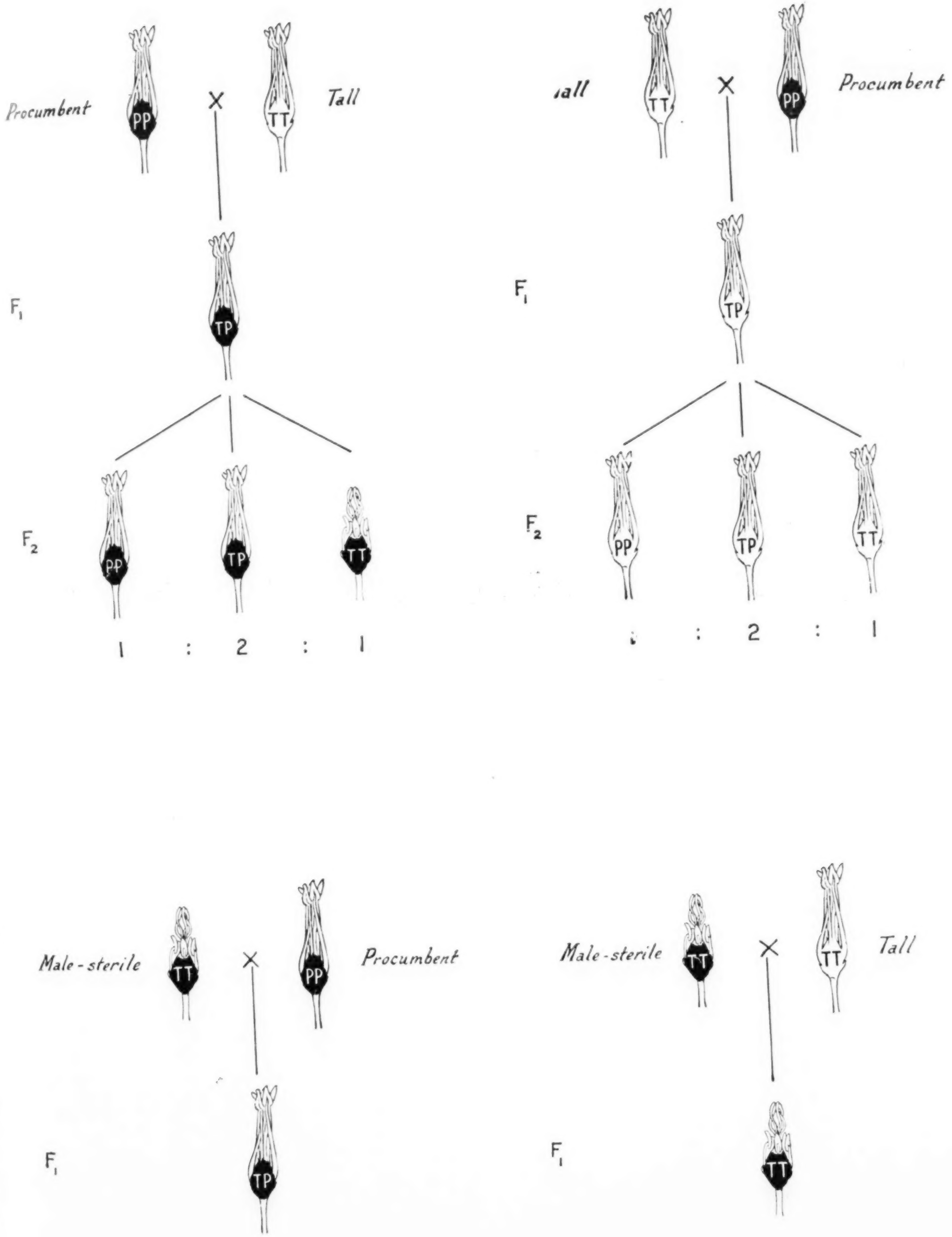
Other Cases of Cytoplasmic Inheritance

It may help to make the position with regard to flax rather clearer if we consider briefly other cases in which it has been suggested that hereditary


● = the cytoplasm, or cytoplasmic constituent of Procumbent
○ = the cytoplasm, or cytoplasmic constituent of Tall
P and T represent corresponding genes, blocks of genes or chromosomes of Procumbent and Tall respectively
= a hermaphrodite
= a male-sterile

KEY TO CHART

Shown on opposite page.



MALE-STERILES APPEAR ONLY IN PROCUMBENT CYTOPLASM

Figure 3

The diagram shows the mode of inheritance of male-sterility, an explanation of the symbols used being found on the opposite page. The shading represents Procumbent cytoplasm, and it will be noticed that male-steriles only appear when the gene T is homozygous in Procumbent cytoplasm. The cytoplasm or cytoplasmic constituent is contributed by the female alone.

characters are transmitted by the cytoplasm as distinct from plastids and chromosomes.

The cases adduced by Loeb, as supporting his hypothesis that the determiners in the chromosomes only act by impressing varietal characters, while the cytoplasm is the real organism in the rough, have been shown to be capable of bearing another interpretation. For instance the fact that in sea urchins the early embryonic growth is always purely maternal in character, and the effect of the paternal chromosomes is not shown till the pluteus stage can be explained by the effect of the maternal diplont or haplont on the egg cytoplasm, a certain "time of action" (Uda and Huxley) being required before the paternal genes can express themselves.

Cytoplasmic, as distinct from plastid and nuclear inheritance of variegation has been postulated by Correns, Baur and Winge. Correns and Baur suggest that all those cases in which the inheritance of the variegation is maternal are due to cytoplasmic inheritance. Winge criticises the classification of Correns and Baur and states that one could not expect fluid cytoplasm to segregate sharply into large white and green areas as occurs in most cases where the inheritance of the variegation is maternal. He suggests that these cases are due to the maternal transmission of plastids, but that a case of variegation in *Humulus* and one in *Capsicum* where there is no production of pure white or pure green branches are the result of cytoplasmic inheritance. Nevertheless Winge himself assumes a partial somatic segregation of cytoplasm to give the white areas found on the leaves of these plants.* In the only paper of his which I have had an opportunity of seeing, however, there is no evidence that the variegation is not due to disease as in the case of *Abutilon*.

Goldschmidt at first reported that the intersexes obtained when crossing geographic races of *Lymantria dispar* were due to cytoplasmic inheritance or to the effect of the Y chromosome, since they were transmitted through the egg-cell alone. He now seems to have definitely decided that in all cases the intersexuality is due to the prezygotic effect of the Y chromosome and that certain female-producing substances are therefore always present in the cytoplasm of the egg. In view of the results in flax, where there is no complication due to the presence of the Y chromosome, it appears probable that Goldschmidt's material could be explained, as he at first thought, as a case of cytoplasmic inheritance.

The examples of cytoplasmic inheritance in plants provided by instances of anisogeny, of which flax has been taken as an example, are of especial interest as they suffer from few of the disadvantages such as complications introduced by the presence of a Y chromosome, or the possible alternative explanations which cannot be excluded by experiment, and are met with in other cases. The facts suggest that:

(a) the cytoplasm, or some cytoplasmic constituent other than the plastids, has individuality and is inherited for an indefinite number of generations so far as is at present known only in the female line, i. e., a third mechanism of inheritance exists, the cytoplasmic as opposed to that of the plastids and nucleus.

(b) Species and even races may differ in cytoplasmic as well as in nuclear constituents.

(c) Like the chromosomes, the cyto-

*Of course, the *Humulus* variegation need not necessarily be due to the partial somatic segregation of cytoplasm as suggested by Winge. It may be that the general cytoplasmic condition of the plant is such that in reacting with the nucleus it produces variegation, just as the nuclear condition in *Tropaeolum* may be such as to produce variegation without any actual somatic segregation.

plasm is capable of variation and may have a definite effect on the ultimate result of the reaction of nucleus and cytoplasm.

AUTHOR'S NOTE: Since this paper was prepared, a very complete account of a similar case of cytoplasmic inheritance in Epilobium (Lehmann and Schwemmle 1927), published about the same time as the case described by Chittenden and Pellew, 1927, has come to my notice.

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AN AGE OF GENIUS

"ENGLISH literary criticism lies under the disgrace of accepting Shakespeare, the tenth-rate player, as Shakespeare, the divine author, and so long as a mistake of this magnitude is admitted into the canon, nobody of any conception can treat the canon with respect. My theory of authorship is simple, rational and within the support of common experience. All it requires is that we assume that Shakespeare, the theater manager, had on his advisory staff or within call a wonderful dramatic genius, whose name we do not yet know; that this genius was as modest as he was wonderful and as adaptable as he was original, and that, of the plays passed to him for licking into shape (plays drawn from Shakespeare, the actor-manager's store), some he scarcely touched, others he changed only here and there, while a few, the few that appealed to his 'fancy,' he completely transformed and recreated in his own likeness. There is nothing incredible, nothing even requiring much subtlety to accept, in this hypothesis. The Elizabethan age was a strange age. It had very little of the passion for self-advertisement that distinguishes our own. It contained many anonymous geniuses, of whom the obscure translators of the Bible were only one handful. The author of the plays may well have been one of the number—a quiet, modest, retiring sort of man, thankful to be able to find congenial work in reshaping plays to his own liking. That, at any rate, is my surmise, and so far from thinking the theory unimportant, I believe it throws a beam of light on the psychology of genius during the Elizabethan age."*

If genius were common enough it would not be distinguished. The England of Elizabeth was "a nest of singing birds," but the mockingbird escaped recognition. "Sweetest Shakespeare, Fancy's child," yes—but *whose* fancy? Was the greatest master of expression so completely overlooked by his contemporaries, or was he keeping out of sight?

The problem of genius would be simplified if we could believe that Bacon wrote Shakespeare in addition to his admitted attainments, that ranked him as the "wisest, wittiest, meanest of mankind." Two transcendent geniuses turning up at the same time and living in the same city, but not meeting or recognizing each other, are more difficult to credit than one legal and philosophic genius who wrote poetry on the side, applying in his writings his amazing fund of legal and philosophic knowledge. Bacon's prominence in other ways may have given him good reasons for refusing to be known as a poet. It must be admitted that literary criticism lacks something if it cannot tell us whether Bacon wrote Shakespeare, but genius may be necessary to

*Orange, A. R., 1822. *Readers and Writers,* p. 122.

appreciate genius. It is a matter of prime interest for eugenics to know how great the human mind can be.

Bacon had special heredity, education and experience to explain his attainments, while Shakespeare, with no such opportunities, is assumed to have developed the same mental equipment as Bacon, covering the full range of legal, linguistic and scientific knowledge. This is too much to take for granted in eugenics, that a mind without learning or scholarship should handle the whole armory of knowledge, thought and sentiment, and should be endowed with a consummate skill of expression, so that the matter and the manner are alike unique and unapproached by any other of his time, except the preeminent Bacon.

The best parallel is Goethe, and when his accomplishments are appraised it seems trivial to object that Bacon was too busy with politics and philosophy to have framed "the vast and complicated creations of Shakespeare." These show in reality very little of deliberate contrivance of plots or incidents. They are remarkable chiefly for the free fancy and the broad understanding of human nature that were allowed to play over the face of history and the dramatic efforts of the earlier writers. As Bacon observed, "Stories invented for the stage are more compact and elegant, and more as we would wish them to be, than true stories out of history." It is the wonder and charm of the Shakespeare literature that it appears to have been so spontaneous and unstudied, as though written merely for diversion, at high speed, and with slight effort. Yet the changes made in later editions show that the author was not careless of the quality of his work.

If there was a Shakespeare genius who eluded the world, "a modest, retiring sort of man" would hardly meet the requirements. No poet has avowed a higher appreciation of his own ability.

> Not marble, nor the gilded monument
> Of princes shall outlive this powerful rime.
> Gainst death and all oblivious enmity
> Shall you pace forth, your praise shall still find roome,
> Even in the eyes of all posterity
> That weare this world out to the ending doome.

Plainly it is not modesty, but pride, that forbids the poet to claim any of the immortality that he boastfully undertakes to confer. He loves his poetry, but is ashamed to father his own child, and ashamed of being ashamed.

> My name be buried where my body is,
> And live no more to shame nor me, nor you.
> For I am shamed by that which I bring forth,
> And so should you, to love things nothing worth.

A strange contradiction for an immortal poet to despise his work, but one could hardly be Shakespeare and Lord Chancellor too, and poetry might seem only a dissipation to the imperial philosopher who had announced: "I have taken all knowledge to be my province." Bacon had boundless self-confidence and made a diligent race for power, position and emolument. He was lavish with his friends, employed the best scholars of his day to polish the Latin diction of his scientific works, and published them in numerous editions, fearing that the English language would not survive. The shame of the poetry may be seen as the black shadow of what a great man's public would think of such folly. A small, modest unknown could not have felt those deadly qualms.

If Bacon had such fears, they seem not to have been groundless. He was accused of venality as a judge, offered no defense, and died in disgrace, though his misfortunes did not shake his confidence that his reputation would endure. His will directed, "My body to be buried obscurely," "my name to the next ages and to foreign nations." His years of retirement, from 1621 to 1626, were spent in revising his philosophical works and publishing new editions. A complete edition of the Shakespeare poems appeared in 1623, with extensive revisions and many

(*Continued on page* 350)

ALCOHOL AND EYE DEFECTS

In the Albino Rat (*Mus Norvegicus Albinus*)

FRANK BLAIR HANSON and FLORENCE HEYS
Washington University, St. Louis, Missouri

FIFTEEN rat generations ago a sister and brother, members of an inbred race of rats, were mated and produced a litter of ten young. This litter was divided at random into two groups of five each—one to be subjected to the influence of alcohol and the other to serve as a control on the experiment.

The rats in the alcoholic group were put into an air-tight fume tank over evaporating alcohol. This treatment was commenced at twenty days of age, and continued until the rats were fully adult. The treatment was given daily, Sundays excepted, and the rats were left in the alcohol-saturated tanks until complete narcotization took place.

The behavior of the rats while in the fume tanks was of great interest. The first effect of the alcohol was to stimulate them to tremendous activity. This exhilaration soon passed, however, and was followed by a period of sullenness or even quarrelsomeness. The last period of the treatment was characterized by increasing drowsiness ending in unconsciousness. At this point the rats were removed from the tanks. It often took several hours for the animals to sleep off the effects of the intoxication.

This treatment with alcohol was continued for ten successive generations of rats, all descended from the original pair with which the experiment started. The same number of control generations was raised simultaneously and under the same environmental conditions for purposes of comparison. The experiment has extended over a period of five years and is still running in a modified form.

The alcohol treatment was discontinued at the end of the tenth generation, but five more generations (the eleventh to fifteenth inclusive) have been secured from both treated and control lines. This was done in order to determine what defects, if any, non-alcoholic animals having ten generations of inebriate ancestry behind them would show.

The direct effects of the alcohol upon the tests was disastrous in the extreme. The rate of growth was considerably slower in the alcoholic rats than in their untreated brothers and sisters. There were cases of paralysis and gross tremors. The normally white, well-groomed coats of the animals became discolored and unkempt. In appearance they were thoroughly degenerate.

The eyes of the treated animals exhibited the most striking abnormalities. After only a few treatments many of them became totally blind. The eyes were white and opaque instead of pink and clear. In some cases there was bleeding at the eyes during treatment and in one or two cases the eye balls collapsed. By the time the alcoholic rats were mature and mated nearly all were blind. Many of the opaque lenses cleared up, however, some weeks or months after cessation of treatment.

During the ten generations of treatment 1,688 young were born to the alcoholic parents. Every one of these young, except one male, was born with perfectly normal eyes and all continued to have normal eyes until they themselves entered the fume-tanks for their period of treatment. The one exception to this was a male whose eyes opened January 30, 1925. This rat (No. 2237) was a member of the tenth alcoholic generation. Its left eye-ball was greatly reduced in size, the right

eye was normal. This was the only defective-eyed animal found in the alcoholic lines prior to alcoholic treatment. It was not treated, but was carefully raised, and with the exception of the miniature eye-ball was apparently a healthy normal individual.

This defective-eyed male was mated to two of his sisters, also untreated, and by them sired six litters. These six litters contained thirty-one rats. Each of the six litters so obtained was inbred (sister-by-brother within the litter) and many of their litters were again inbred in the same manner for two generations. Pedigree charts of these matings have been prepared and are available for inspection. All young so produced were carefully inspected for eye defects. None appeared. It seems that the only eye defect arising in the treated line was of a non-hereditary nature.

Defective-eyed Controls

In the control lines two defective-eyed rats were produced. One in the eighth generation and one in the ninth. The defective in the eighth generation was a male whose left eye-ball was nearly or quite absent. The lids never opened and no eye-ball could be detected by running the fingers over the closed lids. This male was mated to two of his normal-eyed sisters and by them produced three litters, one of which contained three males with similar defects, and another litter had one defective-eyed male. Of these four males with eye-defects, one escaped from its cage and was never recovered; the other three were mated to their sisters and became the progenitors of three inbred lines of rats. These lines were carried for three, four and five generations respectively, strictly inbred sister-by-brother, but all subsequent offspring were normal-eyed.

In the ninth control generation a spontaneous eye defect appeared in a male. This was an irregular spotting of yellow covering almost the entire visible eye. There were seven normal males and two normal females in the litter in which this defective male occurred. Both females were mated to their brother with the eye defect which was unilateral. By one sister he had two litters. One of these litters had two normal males and two normal females. These were bred together producing only normal offspring. In the other litter a female with a reduced eye-ball appeared. Mated with her brothers she gave normal offspring, and these normals inbred gave normals.

By the other sister he sired two litters, one of which gave a male with one eye closed and eye-ball lacking, and reduced eye on the other side. This latter defective male was mated both with his defective-eyed half-sister and with a normal-eyed half-sister. Apparently he was sterile for no litters came of either mating, though both females were fertile with other males.

No eye defects of any kind in either alcoholic or control lines have appeared in the interval from the eleventh to the fifteenth generations.

In an experiment covering fifteen generations in time and including some 3,500 albino rats, only three eye defects have arisen. One of these was in the alcoholic line and the other two in the controls. None of the three was in the nature of a gene mutation, or at least it was impossible by the methods of inbreeding used to establish a defective-eyed race.

No matter how badly injured by the alcohol fumes were the parents' eyes, there was no power to reproduce these acquired defects in the young. In other words, it is relatively easy to render blindness among rats by the direct application of alcoholic vapors, but apparently very difficult, if not impossible, to modify the hereditary capacity of these animals to produce normal-eyed offspring. All the individuals of the ten treated generations and of the five untreated generations following had normal eyes up to the age when they themselves underwent treatment with the one exception of Male No. 2237, as described above and this defect was not hereditary.

Apparently in the albino rat it is not possible to transmit by heredity the eye defects induced by direct contact of the eye with alcohol fumes.

That this experiment covers a considerable period of time in rat history is indicated when translated into human generations and years. Allowing three generations to the century, an experiment of equal duration in man would have begun five hundred years ago or half a century before Columbus discovered America. If within a single human family line half of the individuals born in every generation from 1427 A. D. to 1927 A. D. had been under the influence of alcohol daily from the age of weaning until maturity, that would constitute an experiment somewhat comparable in extent with the one herein reported for albino rats.

Other Experiments

Two brief references to the spontaneous appearance of eye defects in mice are recorded in recent literature. Pearson[10] has described a strain of white mice in which the eye-ball is reduced in size and the lens is opaque. About one and one-half per cent of the mice show these defects. Pearson says the evidence suggests definite hereditary defects. The defect appeared spontaneously, i. e., without a known cause. The mice were not being experimented with to induce abnormalities.

Jones[7] has a preliminary report of a mutation in mice called *r*, reduced. Both lens and eye-opening are affected and total blindness sometimes occurs. The indications are that it is a recessive, sex-linked character; but since no true breeding strain of abnormal-eyed animals has been secured, modifying factors may also be involved.

Stockard[13,14] has the credit for first using the inhalation method in administering alcohol. The animal chosen by him was the guinea-pig, probably an unfortunate choice of an experimental animal for this kind of work from one point of view; but not so in the light of subsequent investigations on other forms. For as it has turned out the guinea-pig is peculiar among all the species used in the alcohol investigations and the divergence of results secured by Stockard with guinea-pigs and Pearl with fowls was undoubtedly the stimulus for much of the extensive work on the alcohol problem since carried out.

Stockard describes a number of gross abnormalities arising in his alcoholic lines; many of these are transmitted to later generations and when once established may be transmitted through the male line, as well as through the female line. Paralysis agitans, anophthalmic monsters, deformities of the hind legs, gross tremors, etc., are some of the defects exhibited by the descendants of alcoholized guinea-pigs. In addition to the anophthalmic monsters just mentioned, other eye defects such as opaque cornea, cataract, small defective eyes, complete absence of one eye and finally of both eyes are among the striking abnormalities described.

The controls of this experiment have been severely criticized. However, such as they are, the controls did not show these defects, and it is more in line with the facts to interpret the exceptional conditions in guinea-pigs as due to some peculiarity of this species in its reaction to alcohol.

Stockard[11,12] was successful in obtaining closely similar eye conditions by treating the eggs of fish directly with solutions of alcohol, and also was partially successful in treating hens' eggs with alcohol fumes either before or during incubation.

Pearl[9] reports an extensive experiment on the effects of alcohol on fowls. He studied growth, fertility and the sex-ratio. He paid particular attention to the appearance of physical deformities since this was one of the most striking features of Stockard's results on guinea-pigs. In the fowl nothing at all comparable to the defects in guinea-pigs was obtained. Pearl says that in any extensive poultry breeding operation a certain small number of crippled and weak chicks will

be hatched. In his treated lines the proportion of defective chickens was no greater than the number produced from untreated parents.

Pearl's results are in line with all other work on the subject except those of Stockard. It seems that in almost any species a certain small percentage of defective individuals will be produced. In order to demonstrate the inheritance of induced eye defects or other abnormalities it will be necessary first to know the normal rate of production of spontaneous defects in the stock employed and then significantly modify that rate by alcohol or other deleterious agent.

Danforth[4] administered alcohol to fowls by the inhalation method. He used animals heterozygous for brachydactyly, polydactyly and color. His data, together with those of Pearl, give conclusive evidence of the selective action of alcohol upon germ cells. No defective-eyed individuals were reported by Danforth.

Bluhm[3] treated white mice with alcohol and claimed that a modification of the sex-ratio resulted. Bilski[2] immersed frogs in alcoholic solutions of different strengths and for different lengths of time. No typical defects were produced by either of these two investigators.

MacDowell[8] treated white rats with alcohol fumes and studied the effect upon the behavior reactions of their offspring in a Watson maze. In the same experiment data were collected on growth and fertility and a careful watch was kept for eye abnormalities, but none appeared.

It seems that alcohol is powerless to induce hereditary eye-defects in the white rat. MacDowell did not have large enough numbers to get the occasional spontaneous eye-defect that on the basis of data presented by Hanson and Heys may occur about once in a thousand rats, for they got three such suddenly-appearing defects in over three thousand animals.

Guyer[5], and in numerous other papers, has described one of the most interesting and valuable of all experiments relating to eye-defects. Two wholly separate lines of defective-eyed rabbits were secured by immunizing fowls against rabbit-lens material and then injecting the blood-serum of such fowls into pregnant does. A third unrelated strain was secured by directly injecting rabbit lens into the pregnant mother. Each of these three defective-eyed strains originated from a single rabbit with abnormal eyes, induced presumably by the serum treatment.

The first experiment may be summarized as follows: Fifteen females received the fowl antigen. Twenty-five matings were made of these fifteen treated females. Sixty-one young resulted. One of these fifteen treated mothers was known as ♀B. In her litter of seven young, one male had the right eye defective and from this single unilaterally defective male a strain of defective-eyed rabbits was started. This line was in the seventh generation in 1920, and thirty-seven individuals had defective eyes. In the later generations both the proportion of defective-eyed individuals and the severity of the defect increased. Guyer attributes the progressive nature of the defect to the inbreeding practiced.

Female 16A1 is the other of the two females to give defective-eyed young following the fowl-serum injections. This female was treated and mated three times. In the third litter of five young two males had defective eyes. One died early, and the other was mated to his normal-eyed sister. From this male a second line of eye-defect rabbits was produced which was in the fourth generation in the 1924 report.

In the third experiment rabbit-lens serum was injected directly into the blood stream of pregnant mothers. Twenty-three matings of such injected females gave seventy-one young. Two had abnormal eyes, both of the same mother, but from different fathers. One of the abnormal males had a

father related to the defective line and was eliminated. This left one abnormal young out of seventy-one, and he became the progenitor of a third defective strain.

Guyer's experiments may be summarized thus: twenty-six females received serum treatment during pregnancy and produced a total of one hundred and fifteen young. Of the twenty-six treated females only three produced defective-eyed young; and of the one hundred and fifteen young produced by all treated females only five had abnormal eyes. The scores of defective rabbits born during the experiments are all descended from three of these five abnormal young.

Bagg and Little[1] describe the establishment of two strains of defective-eyed mice following X-ray irradiation. The parents were treated with comparatively light doses of unfiltered X-rays on five consecutive days. Their offspring were mated *inter se* and in the next generation the eye defects appeared. This inbreeding continued for ten generations, and in the later generations, in some instances, 100 per cent of the offspring were abnormal. The defect is definitely hereditary; is a mendelian recessive; and constitutes a valid example of the experimental modification of the germ plasm by a physical agent. Other defects of ear, feet, and central nervous system are associated with the eye abnormality.

The experiment is controlled by over 2,000 carefully examined controls. The control mice belong to the same stock as the treated and were inbred to reveal any latent abnormal characteristics. None was uncovered. Other papers by these authors further describe these defective mice.

Hanson[6] reports eye defects appearing in a group of 130 rats exposed to X-rays. The dosage was much greater in nearly all cases than that used by Bagg and Little. Practically all animals were rendered sterile and the eye defects described are the direct effects upon the individuals treated.

In conclusion, it may be pointed out that alcohol has been successful in inducing hereditary eye defects in only one species—the guinea-pig. Extensive experiments and severe treatment (in most cases more severe than in guinea-pigs) have failed to show anything comparable in rats, mice, fowls or frogs. Yet it can scarcely be maintained that alcohol was not the responsible agent in Stockard's experiment. At the present time it is perhaps nearest the facts to state that alcohol plus guinea-pig constitution is one thing, while alcohol plus rat, mouse, fowl or frog constitution is again something else.

Guyer with lens serum and Bagg and Little with X-rays report the other two outstanding pieces of work in which hereditary eye defects apparently have been experimentally induced. Yet even here one could wish that a greater number of successes might have been obtained from the original treatments. The many scores of defective rabbits all go back to three treated females; while Bagg and Little treated twenty males and ten females with X-rays, of which only two were modified by the treatment in a germinal way.

There is, then, evidence that occasionally alcohol, lens serum, X-rays and other agents may modify germ cells, but in the vast majority of cases they do not. On the other hand, untreated stocks throw a small percentage of defective offspring when large numbers are raised.

There still remains the perfect experiment for someone to perform along this line. This experiment will have controls more adequate than those used by Stockard and Guyer. The stock must be as nearly a homozygous strain as is possible with biparental reproduction. And the rate at which the stock produces spontaneous defects must be known. This might be called the "crucial experiment," except that Jennings has practically demolished the idea of the crucial experiment in biology.

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An Age of Genius

(*Continued from page* 344)

plays not published before. This was seven years after Shakespeare's death, and nearly twenty years after he returned to Stratford.

The poetry would not be concealed, but the poet found ways to conceal himself, and did it so well that the world is still guessing after three centuries. Shakespeare died first and the literary disguise was not penetrated by the critics. The scheme was laid too deep, and the plot of immortality went wrong. The rime lives on, perennial and powerful, but the eyes of posterity have no place to rest, no object of commemoration. We do not know who the poet's friend was, nor who the poet was, and are thrown back on conjecture, like paying homage at the grave of an unknown soldier.

Or have we to learn that Bacon repented his vow of anonymity and contrived to tag his poetical progeny with ciphers, in order to cheat the "all oblivious enmity" of future generations of critics? A very great man is beyond the appreciation of his contemporaries. An ascendant scale of ability in future generations is needed, if the past is to live.

In the words of Emerson, "Great men exist that there may be greater men." Bacon and Goethe had also reached the same eugenic conclusion, but it has taken 300 years of scientific progress since the time of Bacon for the world to advance to the plane of eugenic consciousness.

"PERCENTAGE OF BLOOD" AND MENDELISM

Value of "Fractions of Blood" as an Index of the Genetic Constitution of an Animal

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THE term, "three-quarter-blood" (or some higher fraction of blood is in fairly common use, especially among producers of animals. Until the discovery of Mendelism it was rather generally although vaguely believed that such expressions gave a fairly accurate picture of the hereditary composition of the animal concerned. Mating two animals together was conceived to be a process analogous to the thorough mixing of salt and sugar solutions and drawing off a sample of the resulting solution, although the existence of occasional irregularities in this process was accorded recognition by the use of such terms as reversion and atavism. Superficially this is a distinctly different conception of the process of heredity from that afforded by the modern genetics classroom analogies, such as: card-shuffling, coin-tossing, matching strings of beads, drawing black and white beans out of a bag, or working out the factorial composition of an F_2 or back-cross generation from a cross involving one, two, three, or even sometimes four factor pairs. More than five factor pairs are seldom used in classroom problems in genetics because of the extra amount of work involved and because the simpler crosses "illustrate the principles just as well."

For convenience we may refer to the group of more or less well defined pre-Mendelian ideas about inheritance as the "percentage-of-blood" theory of inheritance as contrasted with the present Mendelian or genetic theory of inheritance by discrete unit factors. The two groups of ideas are not so radically different as they may appear at first sight. When only a single factor pair is being considered the percentage-of-blood idea fails completely to make a satisfactory explanation of the phenomena of inheritance. However, the Mendelian students early recognized that when several factor pairs were involved, the percentage-of-blood idea at least furnished a convenient way of describing the average composition of a population. A good recent example of that recognition is to be found in the textbook on genetics by Jones.[1] But nearly always such recognition of the usefulness of the percentage-of-blood conception in describing the average hereditary composition of a population has been qualified by the implied or expressed assertion that such a conception was of little use in describing an individual animal. The reference just quoted is as free from such qualification as any publication by a worker in genetics which has come to the writer's attention. Nevertheless practical breeders continue to figure out the percentage of blood of this or that famous ancestor in the pedigree of an animal which they are contemplating purchasing. Also animal husbandry workers, in publications intended for general distribution direct to farmers, continue to show charts and figures of the various percentages of blood which will result from the continued use of purebred sires as contrasted with the use of grade sires. The purpose of this article is to consider, upon the basis of the known laws of genetics, the reliability of the percentage-of-blood idea as a means of describing *individual animals*.

The necessity for such a considera-

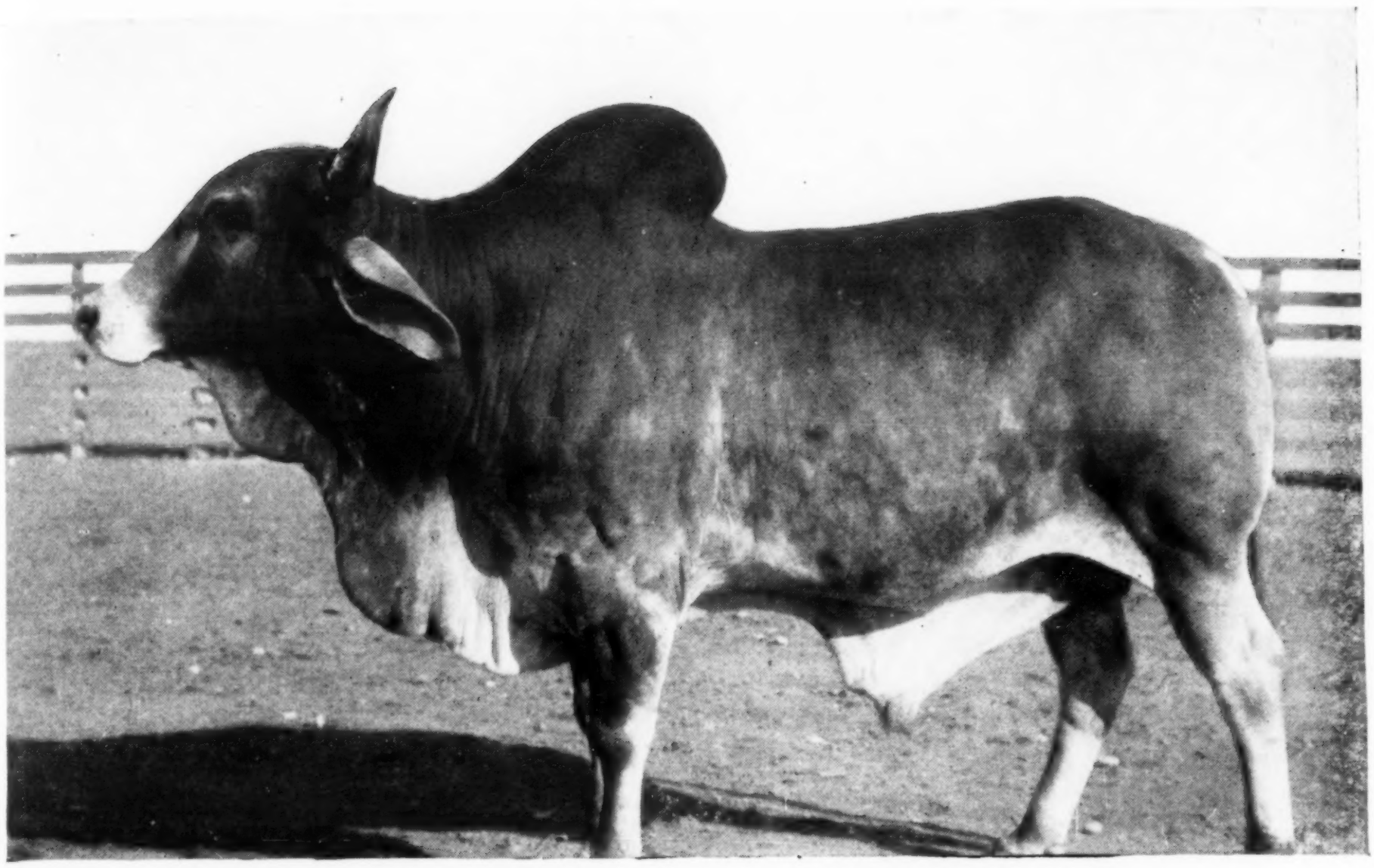
tion was brought forcibly to the writer's attention in studying the problem of what part, if any, Brahman blood should play in the program of the practical beef-producer in Texas. During a visit in 1923 to a number of ranches in the region where Brahman cattle were most abundant it was observed that, to the men who wanted Brahman cattle, the money value of a bull or cow to be used for breeding purposes was highly correlated with the amount of Brahman blood in the animal's pedigree. To be more specific, a prospective purchaser might be considering the purchase of a bull which he supposed to be three-quarter Brahman and for which he would be willing to pay a certain price. Upon learning that the bull was really seven-eighths Brahman instead of three-quarters, he would at once increase his estimate very considerably although the bull before him had not changed a hair between the two estimates. This would not have been surprising if an entire herd of that breeding had been under consideration but when only a single animal was being considered at a time, it seemed to the writer that one of two things must be so; either the percentage-of-blood idea must be a more accurate description of the hereditary composition of an individual animal than was generally indicated in writings on genetics, or these breeders were all of them frequently paying out a considerable amount of money for breeding value which was not actually received. A consideration of the accuracy of the percentage-of-blood description of individual animals was therefore undertaken at the first opportunity and the results of that study have since been compared at every opportunity with field observations and with breeders' ideas and practices.

For those not familiar with Brahman cattle, it may be helpful to explain that breeders of these cattle have been using grades instead of purebreds, because there have not been enough purebreds in the United States and quarantine regulations against animal diseases have prevented further importations of purebreds from India, the native land of these cattle. Scarcely any purebreds are for sale at all, and most of the grades offered for sale do not contain more than three-quarters of Brahman blood. There are enough bulls with seven-eighths Brahman blood to head all the herds which sell breeding animals instead of market animals. A very few fifteen-sixteenths bulls have been sold. However, most of the breeders are confined to a choice between three-quarters and seven-eighths bulls when they must buy new stock and the premium paid for the seven-eighths bulls is large enough that very few producers of market cattle feel that they can afford more than a three-quarters Brahman bull even though they may think that more Brahman blood in their cattle would be very desirable. Since they must usually choose between a three-quarters and a seven-eighths Brahman bull, the precise question before us is "What genetic differences may reasonably be expected to exist between a three-quarter Brahman bull and a seven-eighths Brahman bull?"

Number of Factors Large

The first information any student of genetics would need to have in order to work out the exact answer to this question is a list and description of the genetic factors which differed in the two breeds which were crossed. This information does not yet exist, nor is there even a slight probability that it ever will exist unless some as yet totally unforeseen method of genetic analysis is discovered or genetic research is undertaken on a scale as yet undreamed. Hence the most that one can do toward answering this question is to work out the consequences of this system of mating if different numbers of genetic factors are involved and then to compare those consequences with the actual results seen in field trips and in controlled breeding experiments.

That the races crossed differ in a considerable number of factors is abun-



A FULL BLOODED BRAZILIAN BRAHMAN

Figure 4

The resistance of Braham, or Zebu, cattle to tick fever gives the species considerable importance in tick-infested regions. The scarcity of pure blooded Brahman Cattle makes it necessary for commercial breeding purposes to introduce the desirable characteristics through the use of grade bulls. The genetic significance of the widely used, "fractions of blood" has in such cases much practical importance. Photo from San Rodrigo Ranch, near Del Rio, Texas.

dantly proved by the great diversity of colors, shapes, details of conformation, and dispositions, which is characteristic of all of the crosses but particularly of the three-quarter Brahmans and the one-quarter Brahmans. Moreover, genetic diversity was to have been expected *a priori* from the fact that the two races differ so markedly in so many characteristics. Most systematists classify Brahman cattle and ordinary cattle as belonging to different species although the animals which result from crossing them are as fertile as their parents. The term "race," is probably more accurate than the term, "breed," in this case because several different varieties of Brahman cattle were imported originally and they have been crossed on nearly every breed and variety of cattle found in Texas.

As the simplest possible situation the hypothesis was proposed that the crossed breeds differed in one gene located in each chromosome pair. According to Wodesdalek,[2] there are nineteen pairs of chromosomes in cattle and according to Masui[3] there are seventeen pairs, although judging by what Painter[4] has found in other mammals, one would expect the number to be slightly larger. At any rate it was first assumed that nineteen independent factor pairs were involved in the cross. In order to permit graphic presentation of the results it was further assumed that all these factors lacked dominance and were equal to each other in the effect which they produced. Of course these last two assumptions are probably not strictly true. Some factors from one race are dominant, some from the other race are dominant, and doubtless many others are incompletely dominant; some apparently af-

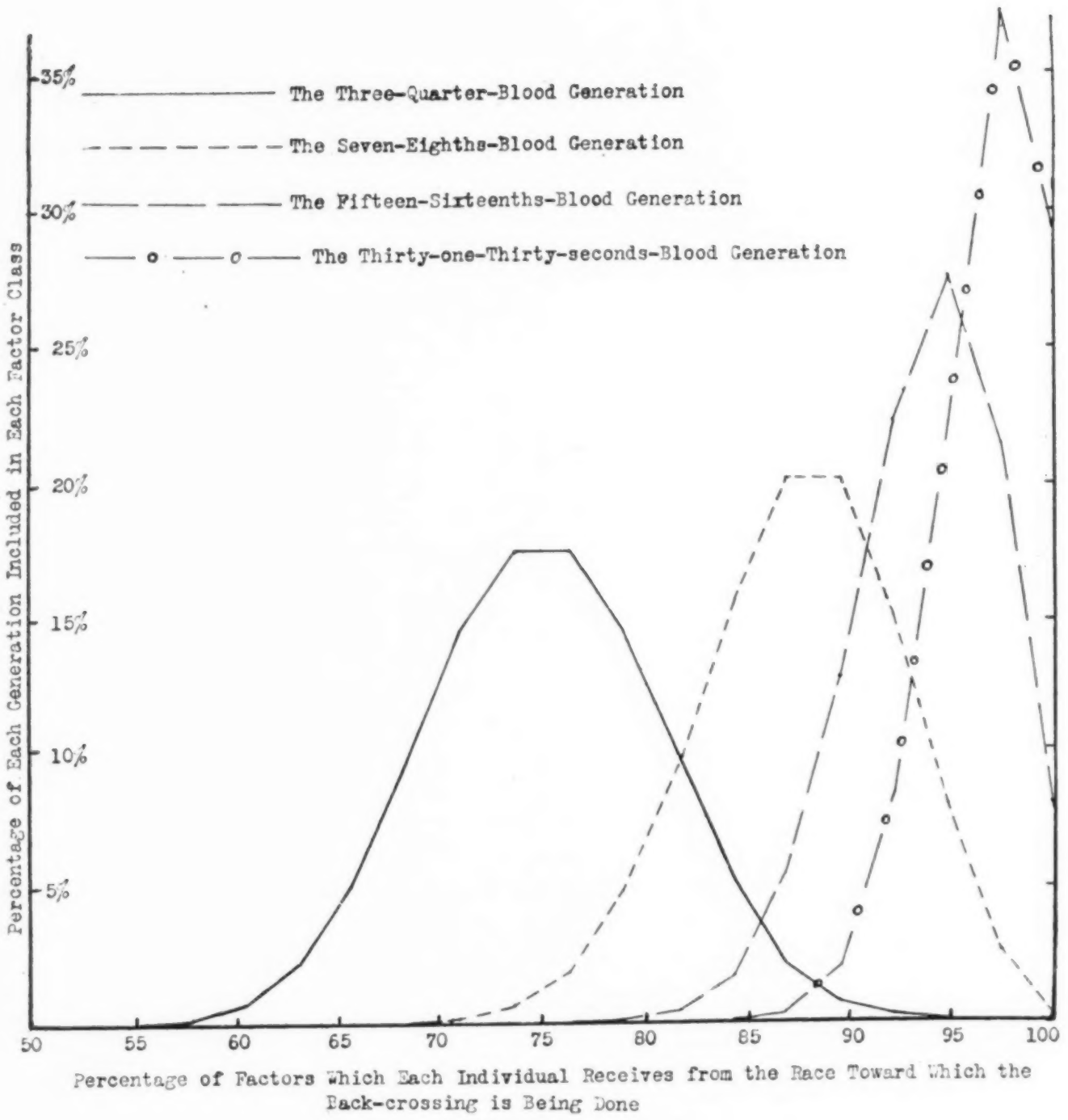

35%
30%
25%
20%
15%
10%
5%
The Three-Quarter-Blood Generation
The Seven-Eighths-Blood Generation
The Fifteen-Sixteenths-Blood Generation
The Thirty-one-Thirty-seconds-Blood Generation
Percentage of Each Generation Included in Each Factor Class
50 55 60 65 70 75 80 85 90 95 100
Percentage of Factors Which Each Individual Receives from the Race Toward Which the Back-crossing is Being Done

Figure 5

The frequency distribution of the different percentages of factors in each of the various generations which would occur in the process of grading up a cross between two breeds which differed in nineteen independently inherited factor pairs.

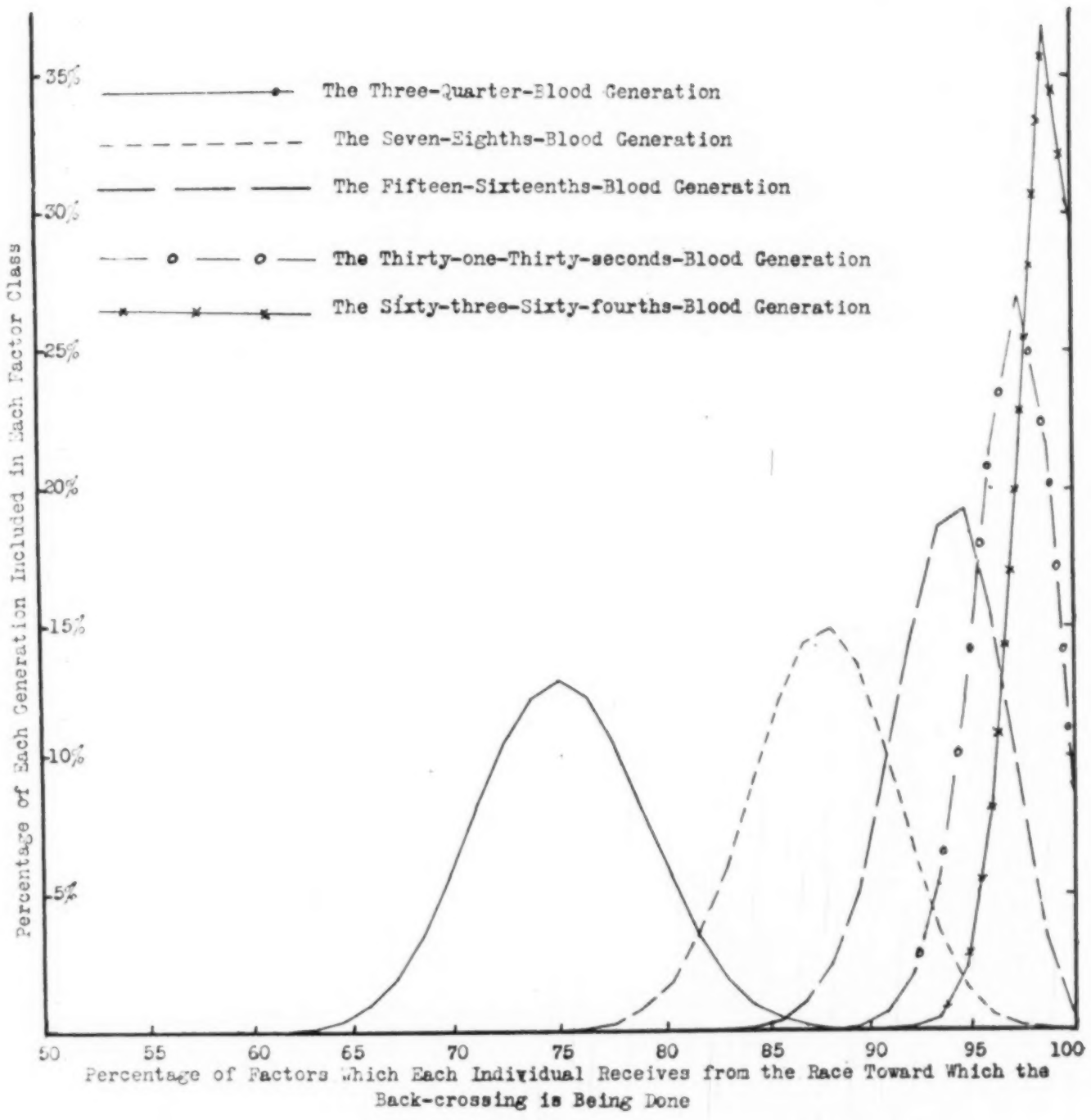


Figure 6

The frequency distribution of the different percentages of factors in each of the various generations which would occur in the process of grading up a cross between two breeds which differed in thirty-eight independently inherited factor pairs.

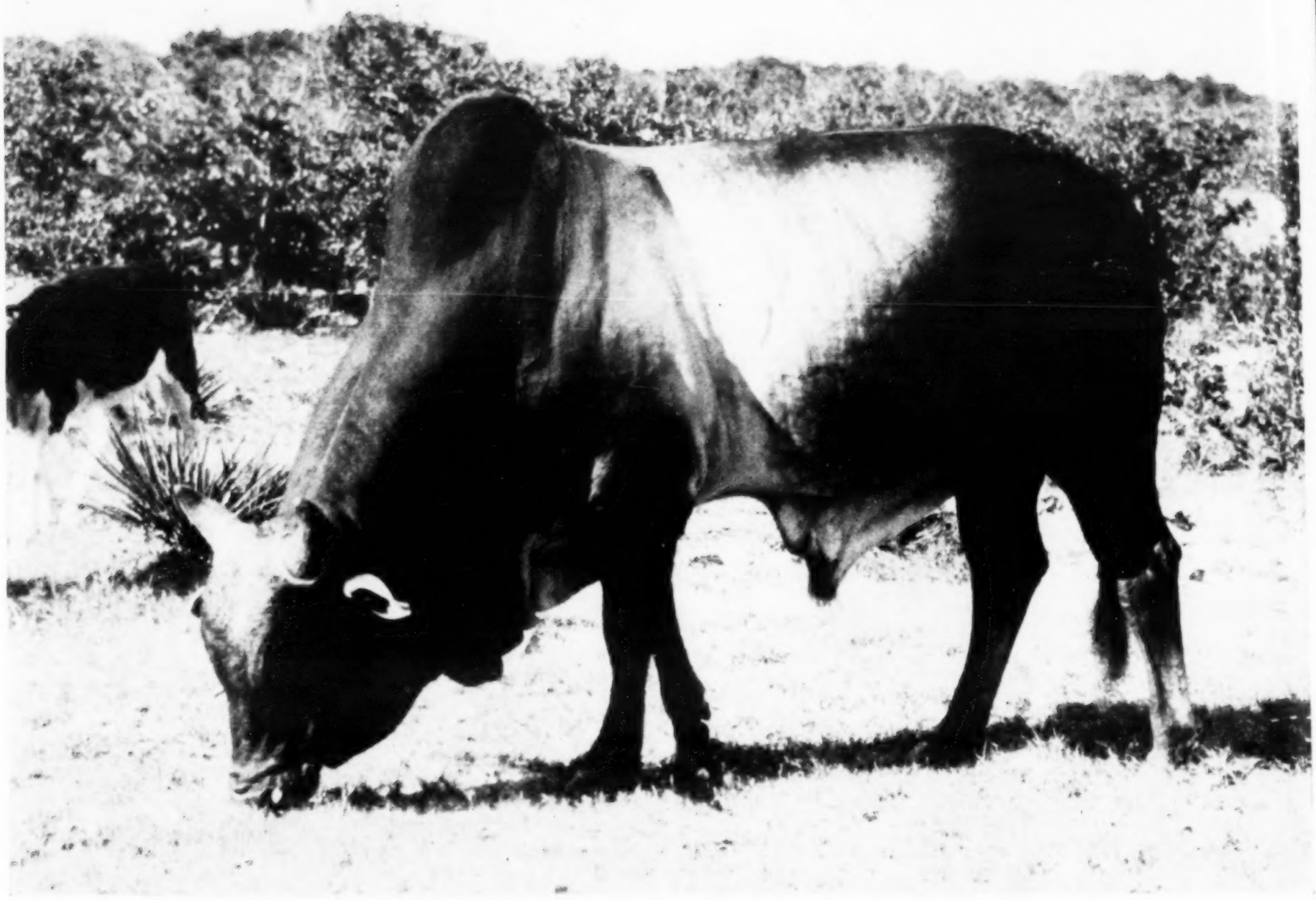
fect only color, others only horn shape, others only the shape and size of the dewlap, hump, or other body parts, etc. However, it should be remembered that the practical breeder must regard the animal and not the factor as the unit in his operations. Inheritance may be and doubtless is by factors but in carrying out mating and selection the whole animal is the unit with which the practical breeder must deal. And when the whole animal is regarded as a unit the effect of a cross involving non-dominant cumulative factors equal to each other in their effects is practically the same as that of a cross involving many pairs of factors showing dominance and having different effects (provided of course that by no means all of the dominant factors come from the same parent). In the latter case the different parts of the animals would show much more variation but the animals each considered as a unit would show little more variation than they would if all the contrasted factors were lacking in dominance, cumulative, and equal to each other in their effects. The hypothesis of non-dominant, cumulative, equal-acting factors was therefore adopted as furnishing a most convenient numerical expression for the animal as a whole and as being in fairly close agreement with the facts of the case when the animal is considered as a unit and when the number of factor pairs is fairly large.

Table I shows the proportions of animals which would have each of the possible proportions of Brahman factors in the first-cross, three-quarters, seven-eighths, and higher grades of Brahman blood. These figures are calculated on the assumption of nineteen pairs of independently inherited factors. Sex-linkage was neglected and, in calculating the composition of the next generation, those types of parents which did not occur in a frequency at least as great as once among twenty thousand individuals were omitted. The results in Table I are shown graphically in Figure 5.

The first-cross animals are of course uniform (at least as uniform as the more variable parent race). The generation produced by back-crossing to the Brahman parent (the "three-quarter Brahman" generation) is of course less uniform than the first-cross generation was and resembles more closely the Brahman parent. Further crossing to the Brahman blood produces of course generations whose uniformity is more nearly equal to that of the Brahman race and which are on the average more nearly like the Brahman race in all characteristics.

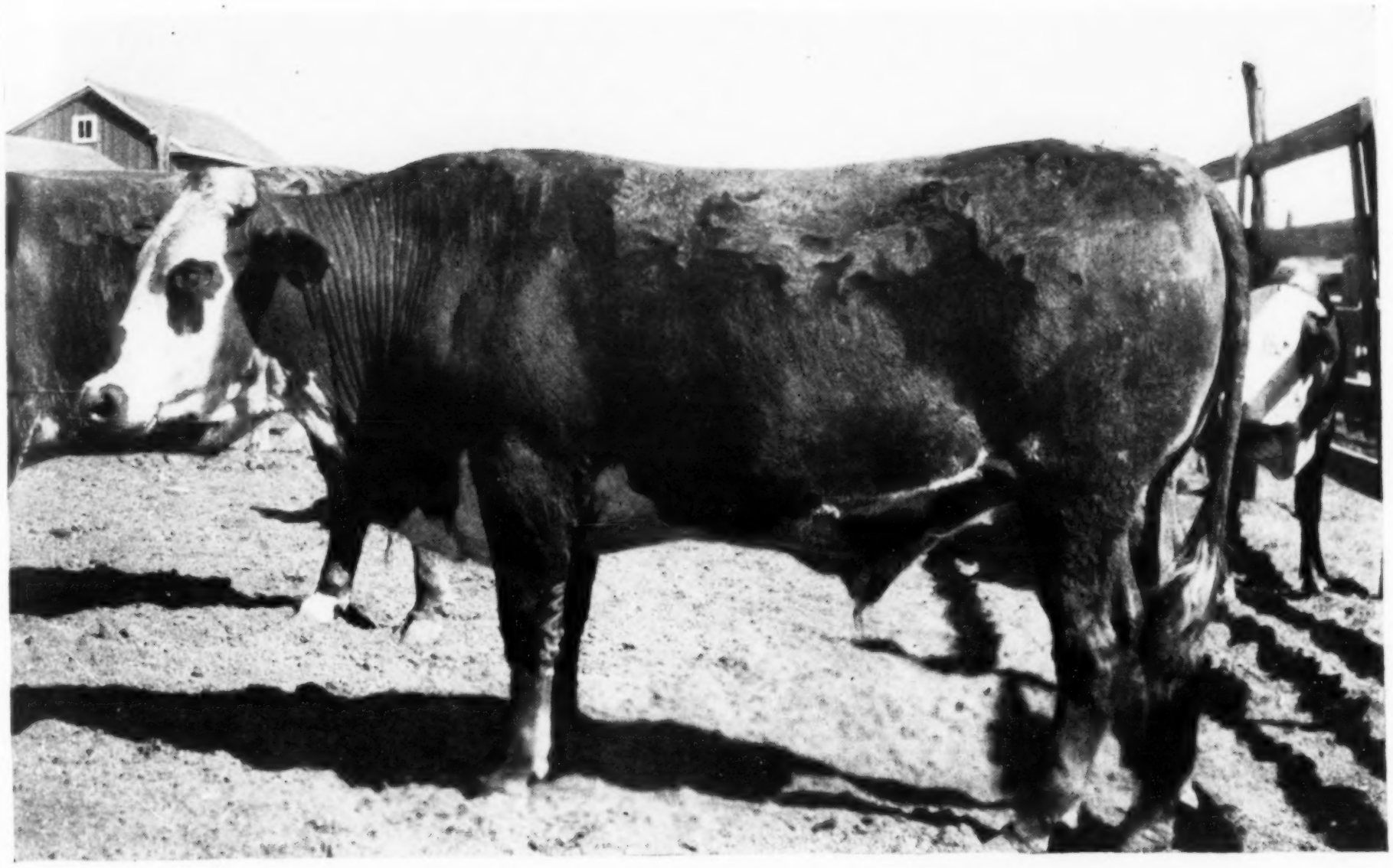
Real Difference Between Grades

It will be noticed from Table I and Figure 5 that there is no overlapping of the first-cross and the "three-quarter blood" generations. Actually, of course, if the figures in Table I were carried out far enough and if Figure 5 were drawn on a sufficiently gigantic scale, some overlapping would be seen. With nineteen independently assorting factors one "three-quarter blood" animal in a little more than a half million (2 to the 19th power) would be expected to have the same genetic constitution as the first-cross animals. Ordinarily in statistical work odds of 22 to 1 (three times the probable error) are regarded as rather convincing and odds of 1350 to 1 (five times the probable error) are regarded as proof positive of a real difference. Here we have a case where the odds are more than a half million to one that any three-quarter blood animal selected at random will have more of the genetic factors of the breed to which it is being graded up than a first-cross animal will. Are not those odds great enough to support the practice of the breeder in placing a higher breeding value on the three-quarter blood animal than on the half-blood, regardless of the visible characteristics of the two animals? When we make the statement (as we sometimes do in lectures on genetics with the object of emphasizing the consequences and importance of segregation) that a three-quarter blood animal can be anything from a halfblood to a pureblood in



SIXTY-ONE-SIXTY-FOURTHS BRAHMAN HEREFORD BULL
Figure 7
Showing the great resemblance to a pure Brahman.

actual genetic composition, we are obviously overstating the case if the number of factors is as large as in this illustration. The statement is true if no limit of the probability of occurrence is placed on it, but without such limits of probability it has little or no practical meaning. Thus in the example given the chances are more than a hundred to one that any random three-quarter blood animal will be homozygous for at least four of the nineteen factor pairs involved in the cross. Also the chances are almost two to one that a three-quarter blood animal selected at random will be homozygous for not less than eight nor more than eleven of the nineteen factor pairs. The percentage-of-blood conception is a more accurate description of the facts of the case than is a Mendelian conception by persons unaccustomed to thinking of crosses involving more than three or four factors. The failure of the percentage-of-blood conception to describe the situation exactly is due to its not including any expression for the amount of variation in the generation described. Thus in this illustration the three-quarter blood animals would all be described as having 75% of the blood of the race to which the grading was being done. Actually 64% of them would have received between 70% and 80% of their genetic factors from that race and 94% of them would have received between 65% and 85% of their genetic factors from that race. So when we say that an animal has 75% of the blood of a certain race we are apt to be close to the truth even for the individual animal, provided of course that the number of factors involved is as large as it is in this illustration. Nevertheless on account of its failure to express the probable variation the percentage-of-blood description is incomplete.

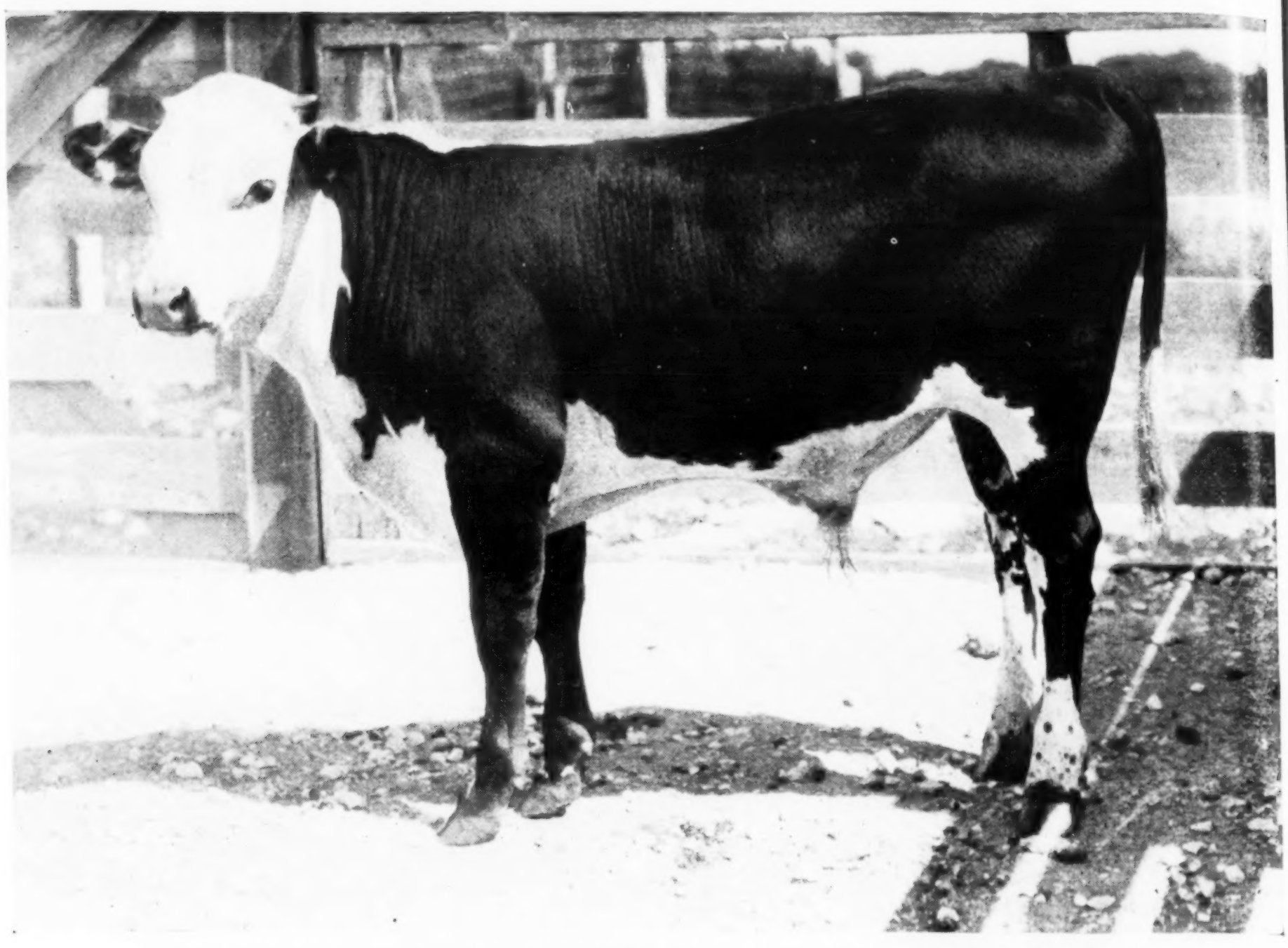


A THREE-EIGHTHS BRAHMAN AFTER FOUR MONTHS FATTENING IN A DRY LOT

Figure 8

The resemblance to the Hereford is marked, though Brahman resemblances are not hard to find. One-half is pure Hereford, and one-eighth grade Hereford.

When we turn to compare the three-quarter-blood and the seven-eighths-blood animals we find that their distributions over-lap considerably. It is true that over 99% of the seven-eighths-blood individuals have received more factors from the race to which they were graded up than the *average* of the three-quarter-blood generation did. It is also true that more than 99% of the three-quarter-bloods have received fewer genetic factors from the race to which they were being graded up than the *average* of the seven-eighths-bloods did. The averages of the two different grades are therefore quite distinct. Nevertheless, there is considerable overlapping between the two curves. About 18% of the area of the lower curve is at or above its intersection with the upper curve and about the same amount of the upper curve is at or below its intersection with the lower curve. The mean of the three-quarter-blood generation lies between 28 and 29 factors or, expressed in percentage of blood, is 75.00% of Brahman blood. The standard deviation is 2.2 factors or 5.7%. The distribution for the seven-eighths-blood generation is slightly skewed and therefore its mean and standard deviation cannot be interpreted quite as literally as those of the three-quarter-blood generation. However, its mean is 87.5% and the standard deviation figured by the ordinary method is 5.0%. The average difference between the two generations is 12.5% and the probable error of that difference for individual animals is 5.1% or less than half the expected average difference. The odds are about nineteen to one that a three-quarter-blood *individual* selected *at random* will possess fewer Brahman factors than a seven-eighths-blood individual also selected at random. The same analysis can be made of the fifteen-sixteenths-blood generation although the increasing skewness of the distribution makes a literal interpretation of the calculated means



THREE-SIXTEENTHS BRAHMAN CALF AT WEANING TIME

Figure 9

The Hereford characteristics greatly predominate. There is considerable overlapping in the appearance of individuals of the various degrees of blood, and the accuracy of this method of classification depends principally on the number of Mendelian factors involved in the cross.

and deviations still less reliable. The average difference between an individual of the seven-eighths-blood generation and an individual of the fifteen-sixteenths-blood generation is 6.25% ± 4.2%. Interpreted without regard to the slight skewness of both distributions, this would mean that in five times out of six in which a fifteen-sixteenths-blood *individual* and a seven-eighths-blood *individual* were selected at random the fifteen-sixteenths-blood animal would carry the larger number of Brahman factors.

Differences of Higher Grades

A similar analysis could be made of the still higher grade generations but the increasing skewness of the distribution would throw more doubt on the validity of the figures thus derived. It is evident that the difference between the average of two successive generations is halved at each succeeding cross as the grading-up proceeds, but that the probable error of that difference decreases at a less rapid rate. Therefore, as the grading-up goes on, not only do the averages of the successive generations become closer together but also there is less and less assurance of the existence of a real difference between two individual animals chosen at random from successive generations. In the illustration just used there is enough such assurance to justify the practical breeders in regarding first-cross, three-quarter blood and seven-eighths blood *individuals* as belonging to genetically distinct groups but it is doubtful whether the probability of a genetic difference actually existing between

two random individuals of successive grades higher than these is great enough to make it worth while to regard them as separate grades instead of lumping them all together as "high grades."

Effect of Increased Number of Factors

In the illustration just given it was assumed that the breeds which were crossed differed in only one factor for each of the nineteen chromosome pairs. Since this is purely assumption it may be worth while to inquire whether the existence of a difference in many more factor pairs would lead to results very different from those just discussed. Perhaps the two breeds differ in hundreds of factor pairs or perhaps in thousands. Linkage, of course, would be presumed to exist between factors whose genes were located on the same chromosome and would thus reduce the proportions of many kinds of recombinations to be expected from any given mating but crossing-over would permit a certain amount of recombination which would thus produce the net effect of a number of independent factor pairs greater than the number of chromosome pairs but less than the number of factor pairs in which the two breeds actually did differ.

For the sake of simplicity let us assume that the net effect of crossing over and of linkage is approximately equal to the situation which would exist if there were exactly twice as many independent factor pairs as there were in our previous illustrations. Table II gives the results to be expected in grading up a cross of two breeds differing in 38 pairs of independently segregating, non-dominant, cumulative factors each approximately equal to each of the others in its effect. Figure 6 shows these distributions graphically.

The generations in Table II and Figure 6 show much smaller standard deviations relative to the total number of factors involved than do the corresponding generations in Table I and Figure 5. However, the corresponding generations have the same mean in both cases. As an inevitable consequence of these two facts the distribution curves for successive generations show less overlapping in Figure 5 than in Figure 6. The mean of the three-quarter-blood generation is 75% in both cases, but its standard deviation is 5.7% when nineteen factor pairs are involved and only 4.1% when twice the number of factor pairs are involved. Likewise the mean of the seven-eighths-blood generation is 87.5% in both cases, but in the first case the standard deviation is 5.0% and in the latter case it is only 3.5%. In the latter case the probable error of the difference between two individuals selected at random, the one from the three-quarter-blood generation and the other from the seven-eighths-blood generation, is only 2.7%. Since the average difference is 12.5% the odds are about 900 to 1 that the random seven-eighths-blood animal will have more of the factors of the race to which it is being graded than will a three-quarter-blood animal selected at random. The odds in favor of this when only nineteen factor pairs were involved were only 19 to 1. This illustrates the greater distinctness of the successive generations from each other where the larger number of factors is involved. The standard deviation of the fifteen-sixteenths-blood generation in Table II is 2.7% and the difference between an individual chosen at random from that generation and one chosen at random from the seven-eighths-blood generation is $6.25\% \pm 2.3\%$ or, in other words, in about 29 cases out of 30 the fifteen-sixteenths-blood animal will have more factors from the race to which the grading up is being done than the seven-eighths-blood animal will. The standard deviation for the thirty-one-thirty-seconds-blood generation is 1.96% and the difference between an individual

chosen at random from that generation and one chosen at random from the fifteen-sixteenths-blood generation is 3.125%±1.7% or in 8 cases out of 9 thus chosen the individual animal belonging to the higher grade would have the larger number of factors from the breed to which the grading up is being done. It thus appears that if there are only nineteen factor pairs involved, it is hardly practical to regard the fifteen-sixteenths-blood individuals as distinct from the higher grades, but that if there are double the number of factor pairs involved, the fifteen-sixteenths-blood individuals can lay good claim to being considered for practical breeding purposes as distinct from the individuals of lower and of higher grades.

More Factors Increase Distinctions Between Grades

It is now in order to consider how these results would be changed if the number of factor pairs concerned in the grading-up process were still larger. For all we know to the contrary the two breeds might differ not merely in nineteen or in thirty-eight but in many hundreds of factor pairs. What effect would such a condition have upon the question proposed here—the reliability of the percentage-of-blood description of an individual animal produced in a grading-up system?

It is not necessary to work out the detailed results of another hypothetical cross to get this information. If the factors involved are independent, non-dominant and approximately equal in their effects, the standard deviation of the three-quarter-blood generation is equal to one-half the square root of its range, both the range and the standard deviation being expressed in terms of factors. Thus in the cross involving nineteen pairs of factors the full range of the three-quarter-blood generation was nineteen factors or, strictly speaking, the range was from the effects of nineteen factors to the effects of thirty-eight factors. The standard deviation was one-half the square root of nineteen or 2.18 factors which was 5.73% of the total of 38 factors in which the two breeds crossed were assumed to differ. In the cross involving thirty-eight pairs of factors the range of the three-quarter-blood generation was from the effects of thirty-eight factors to the effects of seventy-six factors and the standard deviation was one-half the square root of thirty-eight or 3.08 factors which however was only 4.05% of the total of seventy-six factors involved in the cross. This relation of range and standard deviation arises from the fact that the distribution curve of the three-quarter-blood generation is given perfectly by the expansion of the binomial $(a+b)^n$ in which a=b and n is the number of factor pairs involved. This numerical relation between range and standard deviation in the binomial curve was pointed out many years ago.

Thus it happens that the range varies directly with the number of factor pairs involved but the standard deviation varies only with the square root of the number of factor pairs involved in the grading-up process. When we consider as 100% all the factors differing in the breeds which were crossed the range of the three-quarter-blood generation is definitely fixed at 50% and it thus follows that the standard deviation, expressed as a percentage of blood, must decrease as the number of factors involved increases. There is no limit to this relation. As the number of independent factor pairs approaches infinity, the standard deviation of the three-quarter-blood generation, expressed in percentage of blood, approaches zero. And what of the standard deviations of the higher grade generations? Those bear a constant relation to the standard deviation of the three-quarter-blood generation in any given cross. The ratio of the standard deviation of higher grade generations

to the standard deviation of the three-quarter-blood generation is given by the formula $\sqrt{1-(1-2p)^2}$ in which p is the percentage of heterozygosis in the generation being considered. Thus, in the seven-eighths-blood generation, p equals one-fourth and by substitution we get $\sqrt{1-(1-\frac{1}{2})^2}=\sqrt{1-\frac{1}{4}}=$ .866 and we find in the two examples which were worked out that the standard deviation of the seven-eighths-blood generation is approximately 86.6% as large as the standard deviation of the three-quarter-blood generation. Similar examples might be given for the higher grades. It is evident that the standard deviations of all grades decrease relative to the range as the number of factor pairs involved in the cross increases. So, as the number of factors increases there is less and less overlapping of successive generations and we are more and more justified in regarding the percentage-of-blood description as an accurate description not only of the average of the generation but also of the individuals which compose that generation.

Thus the crux of the whole question of the accuracy of a percentage-of-blood description of individuals is the number of factor pairs involved in the cross. If the number of independent factor pairs were truly infinite the percentage-of-blood description would be perfectly accurate. If the number is as low as thirty-eight the percentage-of-blood description is accurate enough to be of great practical use in the first three grades above the first cross. If the number is as low as nineteen the percentage-of-blood description of individuals is accurate enough for practical use in the first two grades above the first cross. If the number of factor pairs involved is only two or three the percentage-of-blood description, while still accurate as a description of the average of the generations is almost useless as a description of individual animals because the standard deviation is so large relative to the total possible range that there is much overlapping of successive generations.

Essential Similiarity of Two Concepts

Let us return for a moment to the apparently conflicting conceptions of inheritance as mentioned at the beginning of this article, namely as a process analogous to the mixing of salt and sugar solutions and drawing off a sample of the resulting fluid or as a process analogous to mixing black and white beans in a bag and drawing out of the bag at random half of the number of beans. It should be pointed out that there is no fundamental difference between these two illustrations. The apparent difference between them is due solely to the relatively small number of black and white beans in the bag as compared to the truly enormous number of salt and sugar molecules in the mixed solution. The smallest sample we can draw from the solution will contain many thousands or perhaps millions of molecules of each kind. If for some physical reason we found it impossible to draw bean samples of less than a hundred beans, we would not be able to draw a sample containing less than 35% or more than 65% of black beans much oftener than once in a hundred trials. If there had to be a million beans in the sample we would not be able to draw a sample containing less than 49.8% or more than 50.2% of black beans oftener than once in many hundreds of trials. Conversely, if it were physically possible to draw samples containing only four or five molecules from the mixed solution we would frequently get samples containing no salt molecules and samples containing no sugar molecules.

Many Factors Involved in Breed Crosses

Since the number of factors involved in any cross is so important in determining the practical results of the cross and the results of systems

of subsequent mating, it may be well to inquire as to the number of factors usually involved in a cross between two breeds of livestock. Accurate detailed information on this subject is almost entirely lacking and, as far as we can foresee, such information will not be available in the near future and perhaps never. However, we are not reduced entirely to idle speculation on this subject for there are many indications that the number of Mendelian factors differentiating breeds of livestock is rather large. To begin with there is the fact that a considerable number of factors have already been found. For the most part these have been factors governing color or hair length or some peculiarity of body conformation, such as dwarfness, notches in ears, presence or absence of horns, defects in hair, and the like. In the second place there are the rather small number of carefully controlled cross-breeding experiments in which the data bearing on body size, early maturity, milk production, and other such economically important characters are usually interpreted by the investigator as indicating that multiple factors are responsible. In the third place, there is the uniformity of a breed when its individuals are contrasted with those of other breeds and in spite of that there is the undoubted diversity within the breed which is apparent whenever we focus our attention upon the individuals of a single breed. Probably the most definite proof of this comes from the biometrical work upon the milk and fat records of cows where rather high correlations are usually found between closely related individuals, thus indicating the existence of many Mendelian factors differentiating individuals and families within the breed. Of course, it is probably true that breeds are not so uniform or so distinct from each other in these physiological characters as they are in color and in economically unimportant details of conformation. Nevertheless, for example, if it is true as we are told that on the average Jerseys give milk less highly colored but richer in fat than the milk of Guernseys and that each of these characters is probably determined by multiple factors, then there is some justification for thinking that there are a considerable number of factors common to Jerseys but not shared by Guernseys and vice versa. Other animals offer illustrations which are none the less real but are less satisfactory because not so readily subject to quantitative study. Thus each of the three leading beef breeds in this country has its own characteristic size and body shape and yet each of those breeds lacks much of complete genetic uniformity as witnessed by the parent-offspring and other close family resemblance which every careful judge knows usually exist. The very existence of distinct families, strains, or tribes, within the breed testifies that the breeders using those terms recognize the existence of genetic diversity within their breed. Yet their insistence upon the virtues and prepotency of their breed in crosses with grade or mongrel animals testifies also to their belief that their breed is vastly different from other breeds and is homozygous for a very great many factors which most other animals of that species lack. Of course the mere fact that breeders believe in the existence of genetic differences within the breed and of much larger differences between breeds does not make that condition a fact but it may perhaps be considered as contributory evidence bearing on the case. In the fourth place, the very condition which caused the writer to study the problem which is the subject of this article may be regarded as evidence that the number of factors involved in the crossing of Brahman cattle and the native cattle of Texas is large. The men who are in the business of selling grade Brahman bulls are united in the belief that they can dis-

tinguish half-blood bulls from three-quarter-blood bulls, and nearly all of them believe that they can always distinguish a three-quarter-blood bull from a seven-eighths-blood one, although some breeders stated to the writer that they thought they might on rare occasions be mistaken about that. Most of them would be able to distinguish between groups of seven-eighths-blood and fifteen-sixteenths-blood bulls, but only a very few were confident that they would have much success in distinguishing between individual animals of that breeding. The attitude of most breeders is pretty well expressed in the statement by one breeder that: "After you get more than seven-eighths of Brahman blood, it is pretty hard to tell them apart. They all look pretty much alike." Nevertheless, in buying and selling Brahman breeding stock percentages of blood are figured in sixteenths and thirty-seconds and, more rarely, in sixty-fourths. The writer has only known personally of one case in which the percentage of blood was figured in one-hundred-and-twenty-eighths. In the fifth place, there is the fact that the trend of genetic research in recent years has been toward the discovery and description of Mendelian factors having smaller and smaller visible effects. Accompanying this has been the discovery of more and more factors affecting each character. As the methods of observation and measurement have been refined the discovery of more Mendelian factors has seemed to keep pace with those improvements in method almost perfectly. The statistical study by Myers'[5] of the apparently pure recessives extracted from a tomato cross may be cited as a good example of this trend in genetic research. In this study the application of detailed statistical treatment revealed that the apparently pure extracted recessive individuals in the F_2 generation actually differed significantly from their recessive grandparents in a way which could best be explained as due to a number of factors, each having very small modifying effects on the characters studied. There is no reason to think that genetic research has approached its limit in this trend. On the contrary, there is every reason to think that each new refinement in measuring detailed differences between approximately similar characters will lead to the discovery of additional genetic factors affecting the development of those characters. To use a simple illustration, we often say that the presence or absence of horns in cattle is due to a single-factor pair. Yet everyone familiar with cattle knows that certain breeds are characterized by horns of a peculiar shape or size. Moreover, within each such breed there are some family differences with respect to horn shape or size, and even within families there is a parent-offspring correlation with respect to horn shape and size. Under these circumstances, who will undertake to say how many genetic factors affecting horn development we would find if we had perfect measures for all the variations in horn phenotypes and had an unlimited number of cattle to use in breeding experiments? Certainly, the number of such factor pairs must be large, but how large no one can say.

Probably not one of these lines of evidence can be regarded as completely convincing by itself, but all indicate the same thing, namely, that the usual number of factors in which two breeds differ is enormously larger than the early workers in genetics supposed. The unanimity of agreement of the different kinds of evidence seems to the present writer to fall little if at all short of a complete demonstration of the truth of that statement. If that is conceded, it must necessarily follow that there is considerable justification for the expressions three-quarter-blood, seven-eighths-blood, etc., for describing individuals as well as for describing the averages of whole generations. Of course, those descriptions are imperfect since they contain no expression of the probable variation among individuals of that particular breeding. Nevertheless, they seem to be the best available descriptions in the absence of knowl-

edge of the complete factorial composition of each individual, which knowledge does not seem likely ever to be in our possession. The question as to the smallness of the fraction to which such descriptions are justified depends, as already shown, upon the number of *independently inherited* factors differing in the breeds which are crossed. Now while the total number of factors may be almost infinite, the number of chromosome pairs in each species concerned is definite and does not often exceed about twenty or thirty pairs in our domestic animals if we may generalize slightly upon Painter's findings. If the chromosome theory of inheritance and linkage is correct, this definite and restricted number of chromosome pairs will prevent the standard deviation from becoming as small as it would if all the factor pairs were independent of each other. This effect of linkage sets a limit to the decrease of the standard deviations (expressed in percentage-of-blood) with an increase in the number of factors involved. Just exactly where that limit is will depend of course upon the "length" of the chromosomes, expressed in crossing-over percentages. An average "length" of 100% crossing-over for each chromosome would mean that even an infinite number of factors would give in the three-quarter-blood generation the same standard deviation as would be given by a number of independent factor pairs twice as large as the number of chromosome pairs. Higher percentages of crossing-over would give standard deviations corresponding to larger numbers of factor pairs. Conversely, if the average chromosome "length" were less than 100% crossing-over the standard deviation, even if an infinite number of factors were involved in the cross, would be that of a number of factor pairs greater than the number of chromosome pairs but less than double that number.

It was shown earlier in this paper that in a cross involving 38 pairs of independent factors, the three-quarter-blood, seven-eighths-blood, and fifteen-sixteenths-blood generations were distinct enough from each other and from higher grades to justify for practical purposes the use of these designations as descriptions of individual animals. It seems to the writer probable that even the use of fractions of blood as small as thirty-seconds in describing individuals might be justified in crosses of extremely different breeds, such as we have in the Brahman cattle crosses in the Gulf States. However, in view of what has been reported about the chromosome number in domestic animals and the improbability of the average chromosome "length" being much if any greater than 100% crossing-over, it seems to the writer unlikely that the use of as small a fraction of blood as one-sixty-fourth is justified in descriptions of individual animals, although of course the use of still smaller fractions in descriptions of the averages of large groups of individuals may be useful and accurate.

Selection of Breeding Animals Not Random

From a practical point of view it is also important to remember that the man who purchases a three-quarter-blood bull does not usually make a random selection from the three-quarter-blood generation. As far as his field of selection will permit, he will naturally select an animal which resembles the purebreds as closely as possible in individual appearance. If his field of selection were infinite and if his judgment were perfect and if individual appearance and genotype were perfectly correlated, he might thus select a bull which would be genetically identical with the purebreds. However in actual practice not one of these three conditions will be fulfilled. Because of the large number of factors involved in most of such crosses, the relatively small number of bulls for sale falls far short of offering the prospective buyer the necessary range for selection. Because the buyer's judgment is not perfect, he can not always select from the available bulls the one whose in-

dividual appearance most closely resembles that of the purebreds. Because the animal's genotype and individual appearance are not perfectly correlated, the animal selected will usually resemble the desired type less closely in genotype than in individual appearance. The net result of these circumstances is that the animal thus selected will usually resemble the desired type more closely in genotype than it would if it were selected at random from its generation but will not resemble the desired type genetically as closely as the buyer thinks it should on the basis of its individual appearance. Thus the buyer must expect some regression in the breeding value of his bull toward the average breeding value of the generation to which that bull belongs. The amount of that regression depends upon the three factors just discussed (range of selection available, buyer's judging ability, and closeness of correlation between genotype and individual appearance) and there does not seem to be any practicable way of measuring that regression. Nevertheless a certain amount of regression should be expected by the buyer. That is the real genetic justification for the practice of the buyer in paying considerable attention to the percentage of blood of a particular race or of a particular ancestor in the pedigree of an animal which he is considering buying for breeding purposes.

Percentage of Blood Not an Index of Inbreeding

The writer holds no brief for those who try to measure inbreeding and relationship on a "percentage-of-common-blood" basis instead of using the more accurate but slightly more intricate formulae developed by Wright.[6] The practical breeder, being accustomed to thinking in terms of percentage-of-common-blood naturally will not want to change to a more complicated system unless very greatly increased accuracy is gained thereby. It is also true that relationship between an individual and a direct ancestor will be found to be approximately the same figured by either method, except that a small correction for the degree of inbreeding of the related individuals is neglected in the ordinary percentage-of-blood method. The relationship between an individual and a direct ancestor is the relation in which the average breeder of purebreds is most intensely interested because at present line-breeding is by far the most popular system of breeding. The essence of that form of breeding is to mate together animals each of which has as high a relationship as possible to the famous ancestor toward which the line-breeding is being directed. At the same time it is desired that the two animals mated together should have no relationship (or as little as possible) to each other except through that one famous ancestor. Since the "percentage-of-blood" expression of relationship to a direct ancestor gives values not very different from those given by Wright's more exact formula and is easier for the average breeder to understand, it seems practical for use under ordinary circumstances in guiding a policy of line-breeding but there is need for a clearer appreciation of its limitations when applied to collateral relatives and of its unsuitability as a measure of inbreeding. As an extreme example, the percentage-of-common-blood between full brother and sister is 100% yet the relationship between them is only 50% according to Wright's formula if neither they nor their parents were the result of inbreeding. Mating full-brother to full-sister would produce offspring 100% inbred in the very first generation according to the percentage-of-common-blood method of measuring inbreeding, but only 25% inbred according to Wright's formula.

Summary

This paper presents the results of an inquiry into the accuracy of "percentage-of-blood" descriptions of individual animals in the various generations which are produced in the process of grading-up one breed or common

TABLE I—The Distribution of the Different Phenotypes in the Various Generations Resulting from Grading up a Cross Involving Nineteen pairs of Independent, Non-Dominant, Cumulative Factors Equal to Each Other in Their Effects.

Number of Brahman Factors	First-Cross %	Three-Quarter Bloods %	Seven-Eighths Bloods %	Fifteen-Sixteenths Bloods %	Thirty-One Thirty-Seconds Bloods %
Nineteen	100.00	----	----	----	----
Twenty	----	----	----	----	----
Twenty-one	----	.03	----	----	----
Twenty-two	----	.18	----	----	----
Twenty-three	----	.74	----	----	----
Twenty-four	----	2.22	----	----	----
Twenty-five	----	5.18	.01	----	----
Twenty-six	----	9.61	.04	----	----
Twenty-seven	----	14.42	.18	----	----
Twenty-eight	----	17.62	.66	----	----
Twenty-nine	----	17.62	1.98	.02	----
Thirty	----	14.42	4.87	.10	----
Thirty-one	----	9.61	9.74	.48	.01
Thirty-two	----	5.18	15.74	1.82	.07
Thirty-three	----	2.22	20.23	5.47	.45
Thirty-four	----	.74	20.23	12.77	2.25
Thirty-five	----	.18	15.17	22.35	8.42
Thirty-six	----	.03	8.03	27.60	22.30
Thirty-seven	----	----	2.68	21.47	37.16
Thirty-eight	----	----	.42	7.91	29.34

TABLE II—The Distribution of the Different Phenotypes among Various Generations Resulting from Grading Up a Cross Involving Thirty-Eight Pairs of Independent, Non-Dominant, Cumulative Factors Equal to Each other in Their Effects.

Number of Brahman Factors	First-Cross %	Three-Quarter Bloods %	Seven-Eighths Bloods %	Fifteen-Sixteenths Bloods %	Thirty-One Thirty-Seconds Bloods %	Sixty-three Sixty-fourths Bloods %
Thirty-eight	100.00	----	----	----	----	----
Thirty-nine	----	----	----	----	----	----
Forty	----	----	----	----	----	----
Forty-one	----	----	----	----	----	----
Forty-two	----	----	----	----	----	----
Forty-three	----	----	----	----	----	----
Forty-four	----	----	----	----	----	----
Forty-five	----	----	----	----	----	----
Forty-six	----	.02	----	----	----	----
Forty-seven	----	.06	----	----	----	----
Forty-eight	----	.17	----	----	----	----
Forty-nine	----	.44	----	----	----	----
Fifty	----	.98	----	----	----	----
Fifty-one	----	1.97	----	----	----	----
Fifty-two	----	3.52	----	----	----	----
Fifty-three	----	5.63	----	----	----	----
Fifty-four	----	8.09	----	----	----	----
Fifty-five	----	10.47	.01	----	----	----
Fifty-six	----	12.22	.02	----	----	----
Fifty-seven	----	12.86	.05	----	----	----
Fifty-eight	----	12.22	.15	----	----	----
Fifty-nine	----	10.47	.40	----	----	----
Sixty	----	8.09	.92	----	----	----
Sixty-one	----	5.63	1.93	----	----	----
Sixty-two	----	3.52	3.61	.01	----	----
Sixty-three	----	1.97	6.07	.04	----	----
Sixty-four	----	.98	9.11	.12	----	----
Sixty-five	----	.44	12.14	.38	----	----
Sixty-six	----	.17	14.31	1.05	.01	----
Sixty-seven	----	.06	14.81	2.53	.04	----
Sixty-eight	----	.02	13.33	5.31	.16	----
Sixty-nine	----	----	10.32	9.59	.64	.01
Seventy	----	----	6.77	14.68	2.09	.09
Seventy-one	----	----	3.69	18.68	5.69	.52
Seventy-two	----	----	1.63	19.23	12.55	2.39
Seventy-three	----	----	.56	15.39	21.52	8.47
Seventy-four	----	----	.14	8.98	26.90	21.89
Seventy-five	----	----	.02	3.40	21.81	36.68
Seventy-six	----	----	----	.63	8.61	29.93

stock by the use of sires belonging to another pure breed. The accuracy of such descriptions is found to depend upon the number of pairs of factors which differ in the cross. If only one factor pair were involved they would have no meaning at all as descriptions of individual animals. If as many as nineteen independent factors are involved and if the whole animal is considered as a unit, percentage-of-blood descriptions are accurate enough to justify their use for three-quarter-blood and seven-eighths-blood individuals but are not accurate enough to be of much use in describing individuals differing only one-sixteenth in blood. If twice that number of independent factors is involved the percentage-of-blood description is accurate enough for use in describing the fifteen-sixteenths-blood generation but is not accurate enough to be of much use in describing individuals which differ by one thirty-second in blood. The existence of linkage and a definite number of chromosome pairs places a limit on the smallness of the fraction of blood which one is justified in using to describe an individual, even though the number of factors involved in the cross may be almost infinite.

The use of the percentage-of-common-blood method of measuring relationship between two individuals does not lead to very serious errors when one of the two individuals is a direct ancestor of the other, but does give rise to serious errors when applied to individuals which are collateral relatives of each other. Measuring an animal's degree of inbreeding by the percentage of blood common to its sire and dam is not accurate enough to be of much practical use.

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Biological Miracles

AFTER a lapse of several decades the task of acquainting the layman with the progress of science has again been taken up with intelligent effort. The task is no simple one, and that it is undertaken at all is due to the broad vision of those few professional men who have the ability to present technical matters in an attractive form and who also appreciate the desirability of a rapid and widespread dissemination of the discoveries made in science.

It is a real pleasure to direct attention to the *Essays in Popular Science* by Julian Huxley, the grandson of that former distinguished champion of lay education.* Professor Huxley is under no illusions as to the effect of modern civilization upon the processes of cerebration of the average man. "There is a danger, in these days of manifolded information and broadcast amusements that the world will become divided into those who have to think for their living and those who never think at all. . . . the occupation by which the average man is gaining a livelihood is becoming more standardized in its condi-

(*Continued on page* 370)

*Huxley, Julian. *Essays in Popular Science.* Chatto and Windus, London. 1926.

INHERITANCE OF ABNORMALITIES IN TEETH

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Hanover, New Hampshire

THE following cases establish without doubt that some malformations of teeth in mammals are inherited. It is not the purpose here to bring forward a great deal of evidence proving such inheritance but to give a few cases in which heredity has certainly played an important part, and to call the attention of the reader to the fact that in this direction lies a field, as yet little explored, which has a practical as well as scientific interest.

The first case is one cited by Thadani[1] of a type of men called "Bhudas." They are found in India and are hairless and toothless, with extreme sensitiveness to heat. When a Bhuda marries a normal woman all the sons and daughters appear normal. When the sons marry normal women their children appear normal in both sexes; when the daughters marry normal men the resulting daughters are normal but the sons are Bhudas.* No case is on record yet where a toothless man married the daughter of a Bhuda, nor are there cited any cases where the females have shown this peculiar condition. This, therefore, is a case of sex-linked inheritance in which the abnormal condition is shown in the male, the female being a carrier and not showing the toothless condition unless homozygous for it, and as no cases were reported where a Bhuda married the daughter of a Bhuda, no such female was found. If sex-linked, the children should be normal and are so; the third generation should show the condition only in the males if the mother was a carrier and married a normal man, which the above facts show. Guilford[2], however, tells of a woman (nationality not given) without teeth or hair and having a sister appearing normal in these respects. The one without teeth or hair had a son also lacking teeth and hair. This edentulous son married a normal woman and had eight children, two of which had several undeveloped teeth, but the sex of these children is not stated nor which teeth were undeveloped. The normal sister had eighteen children, one of which showed the toothless and hairless condition, the sex not being stated. This case, even if very incomplete, seems to supplement the case of the Bhudas by showing that it may be possible for this condition to be found in the female. If a daughter of a Bhuda married a Bhuda it would be possible to get a female homozygous for these traits with a sister appearing normal. Therefore, it looks as if the case of which Guilford speaks is very similar to that of the Bhudas.

Another case that has not been worked out but yet shows that some type of inheritance is involved is cited by [3]Sinha, of a Hindoo family in Bengal. A man with noticeably brown teeth married a normal woman with white teeth. Of the children, the first, second, and fourth sons had brown teeth while the third son had white; the first, second and fourth daughters also had brown teeth while the third daughter had white teeth. The first

*This is similar to the inheritance of color-blindness and hemophilia (See *Journal of Heredity* for January, 1925, p. 40.) According to theory we should expect half of the male children of the daughters of "Bhudas" to be normal. The fact that those observed have been toothless is possibly due to the small number of individuals considered.—*Editor*.

son married a normal woman with white teeth, and had, besides a normal son, a daughter with brown teeth. The first daughter married a normal man and had three sons, one having brown teeth; and three daughters all of whom were normal. This case, like many others, only serves to point out the inadequacy of available data, but convinces one that inheritance is the guiding influence.

A case quoted by Cole[4] about defective teeth in Holstein-Friesian cattle lacks sufficient data, but does show decidedly the influence of hereditary factors. Three calves born of normal dams had imperfect incisors similar to the bull who sired them. The normal dentition is four incisors on each side, sharp and well developed. The bull had three small incisors on the left side and two on the right. One calf had two small incisors on the left side and only one on the right. Another, two conical, round, and blunt incisors on both sides. The third had only one small incisor on the left side and one on the right. There was noticed along with the imperfect teeth a lack of hair about the head and neck regions, which, however, later became normal. This case appears to be one of inheritance, for all the calves on this farm were housed and fed alike, thus leaving out the possibility of environmental influence. Only these three showed imperfect teeth. Sex was not mentioned, so probably is not to be considered. The case appears to involve interaction of factors, as the imperfection in each case is not identical, yet very similar.

The normal dentition in humans is two incisors, one canine, the bicuspids and three molars on either side of the jaw in the order named. McQuillan[5] mentions a case where father, son and grandson lacked the lateral incisor of the upper jaw; a second son also had exceedingly dwarfed incisors. The second son married and part of his children had stunted teeth similar to their father's. Only males are reported as having the defect, which might lead one to regard the character as a sex-limited male trait.

Another case which should be mentioned is of the Sioux Indians, which, as a study of skulls has shown, formerly had very well formed jaws and teeth; but McKay[6] has found an extremely high percentage of malocclusions in present-day Sioux. Is this due to the civilization forced on them or to heredity? It probably is safe to conclude that both causes are operating. Some cases are due doubtless to mutilations resulting from extraction and poor dental treatment, which McKay mentions, but heredity also plays an important role; how important is yet to be determined. It is interesting to consider the increase of intermarriage and the tendency to race mixture, which means in many cases the mingling of factors for heavy jaws and teeth with those for more delicate jaws and teeth. It is thus possible for the offspring to inherit large strong teeth with delicate or smaller jaws. The large teeth forcing themselves into the small jaw would tend to distend to jaw and cause malocclusion. C. B. Davenport[7] mentions this possibility in his paper on "The Effect of Race Intermingling."

A young man of my acquaintance has bicuspids in front of his canines, a condition found in his father as well as in two cousins, one of each sex. I mention this case as another of probable inheritance.

Dr. G. T. Norton tells me of a case in which a pegged lateral, a blunt underdeveloped canine, can be traced from a mother to her son and daughter and is apparently inherited.

The cases I have recorded above all show, in some degree, hereditary influence; their extent and importance cannot be determined without more perfect data. They illustrate the limited amount of work done in this direction, yet indicate a field of interest and impor-

tance. A large step towards a fuller knowledge of this subject would be made if dentists should keep a complete record of their patients.

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[3]Sinha, S., Tooth Color, *Journal of Heredity,* 9:pp. 96, February, 1918.

[4]Cole, J. J., A Defect of Hair and Teeth in Cattle, *Journal of Heredity,* 10:pp. 303-306, October, 1919.

[5]McQuillan, J. H., Heredity Transmission of Dental Irregularities, *Dental Cosmos,* Vol. 12, February, 1870.

[6]McKay, F. S., Malocclusion of Teeth Among North American Indians, *Dental Cosmos,* February, 1920.

[7]*Proceedings of American Philosophical Society,* Vol. 61, pp. 364-368, 1917.

Biological Miracles

(*Continued from page 367*)

tions, more limited in its scope, more definite in its routine."

From the standpoint of our own Science Service, so busily engaged in tempering science with journalism the following extract should be of interest:

> In the morning he [the average man] reads his syndicated news and imbibes his millionfold-disseminated opinions. In the evening he goes to the cinema, or turns on his wireless set, or (if rather old-fashioned) manipulates his gramophone; in any case he again receives impressions which are being or have been scattered broadcast to millions of other human beings, and, what is more serious, he is presented with his impressions, whether by newspaper, cinema, radio, or whatever else, in a form demanding the minimum of thought. . . .

Although the average man is in a bad way and rapidly becoming worse, the professionals, too, are not living a full life, a fact that does not escape Professor Huxley and both groups should profit from a perusal of the preface.

The subject matter is a grouping of lectures delivered in England and of articles that appeared in several non-technical periodicals. Those who have read the author's "Essays of a Biologist" will welcome the present volume.

The book covers a wide field, embracing Heredity, Physiology, Psychology, Sociology, Theology, History and Literature.

The biological point of view is maintained throughout and though there is some repetition this is not a disadvantage since a certain amount of reiteration is required to accustom the lay student of biology to many of the terms. Naturally those having a first hand knowledge of the several fields discussed will detect faults, but these are largely matters of order in presentation or perhaps simplifications rather than errors of fact.

The chapters dealing with heredity and the cytological basis of sex determination are clearly and simply written and this despite the fact that the author's special field is physiology. The hypotheses of the linear arrangement of discrete heritable elements in or upon the chromosomes and the chromosomal control of sex are accepted wholeheartedly.

The description of the function of the endocrine glands gives a vivid picture of the internal mechanism controlling vital processes. This chapter should enlighten those among the medical profession who have concluded that there is nothing in heredity—that everything is explainable on the basis of internal reactions.

The essay on the frog is a masterpiece of presentation where abstruse developmental processes are described in an engrossing fashion. The truly astounding things that the physiologists have accomplished with this humble animal constitute real biological miracles. Apparently this grotesque animal can be turned virtually inside out without

(*Concluded on page 374*)

FORMS OF PLANT CHROMOSOMES

Photographs of Some Scientifically Interesting Chromosome Groups

JOHN BELLING
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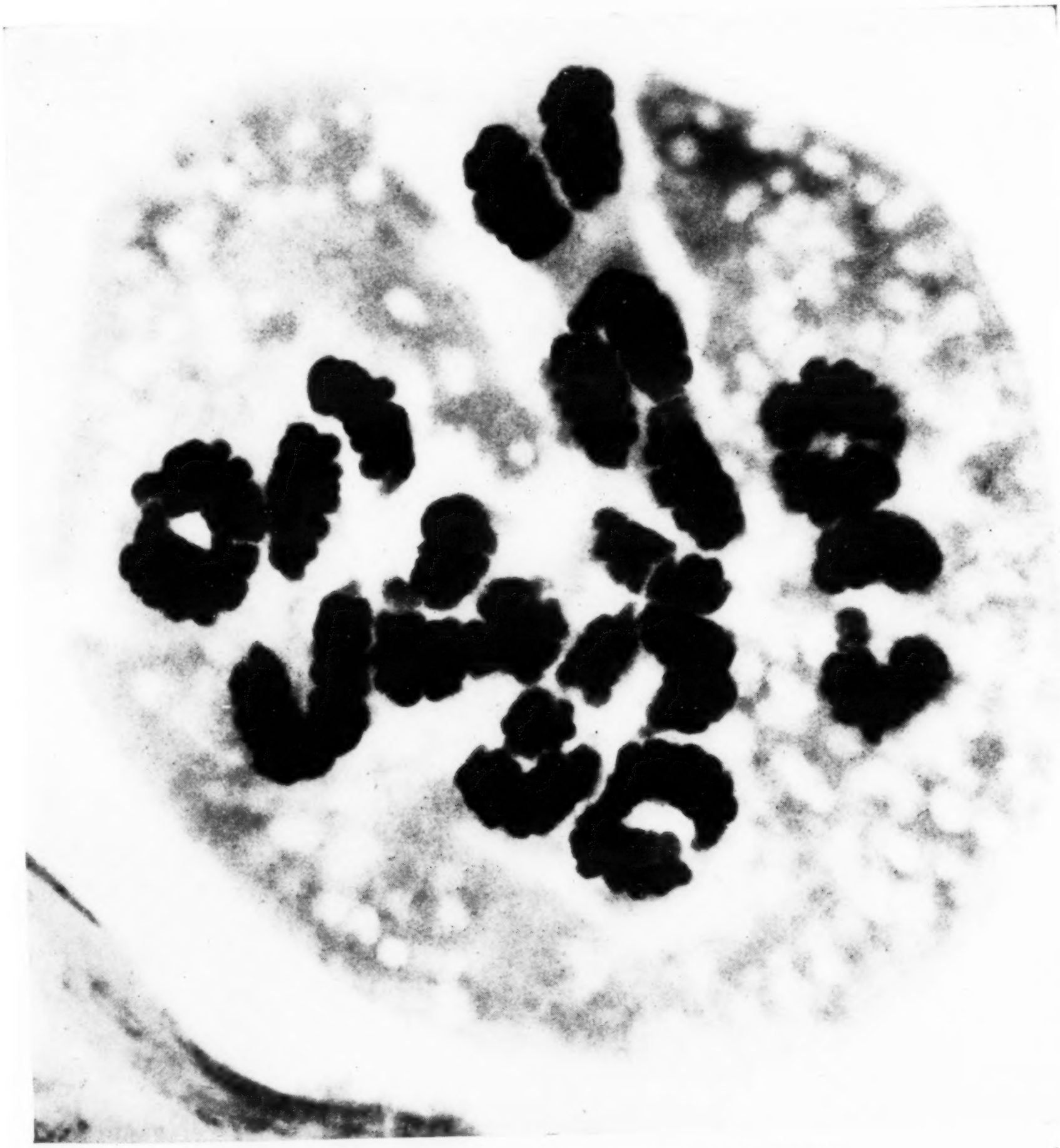
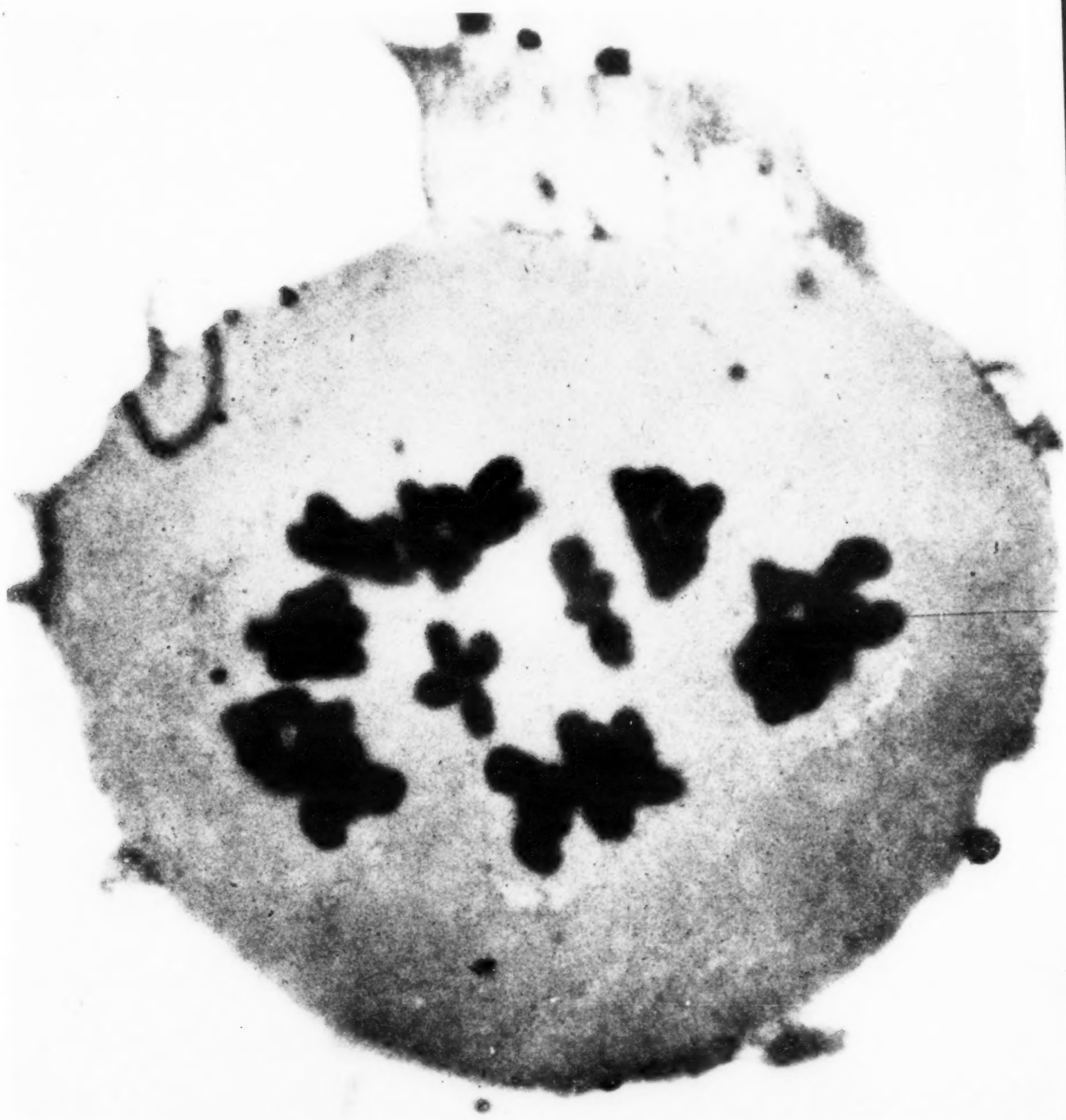


CHROMOSOMES AND CHROMOMERES

Figure 10

Bivalent chromosomes of the spiderwort, *Tradescantia virginiana*. The chromomeres, of which the chromosomes are made up, show especially clearly in this species.

A GROUP of chromosomes is often difficult to photograph, because its members are not usually all precisely in the same plane. This is especially the case with the first division in the pollen-mother-cells, where the maternal and paternal chromosomes are coupled in pairs. Also plant chromo-

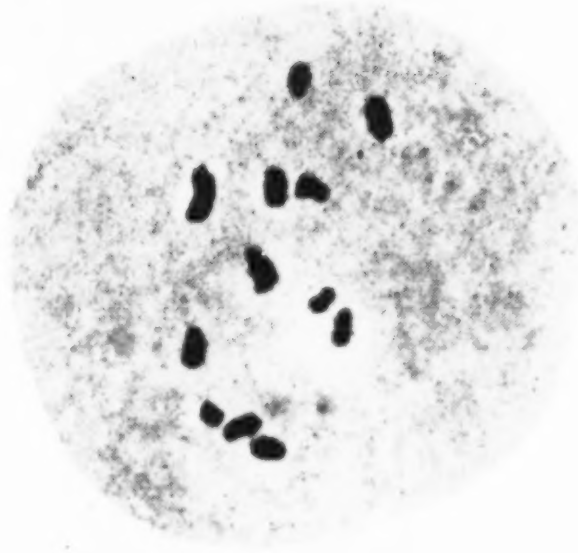


CHROMOSOMES OF THE HYACINTH

Figure 11

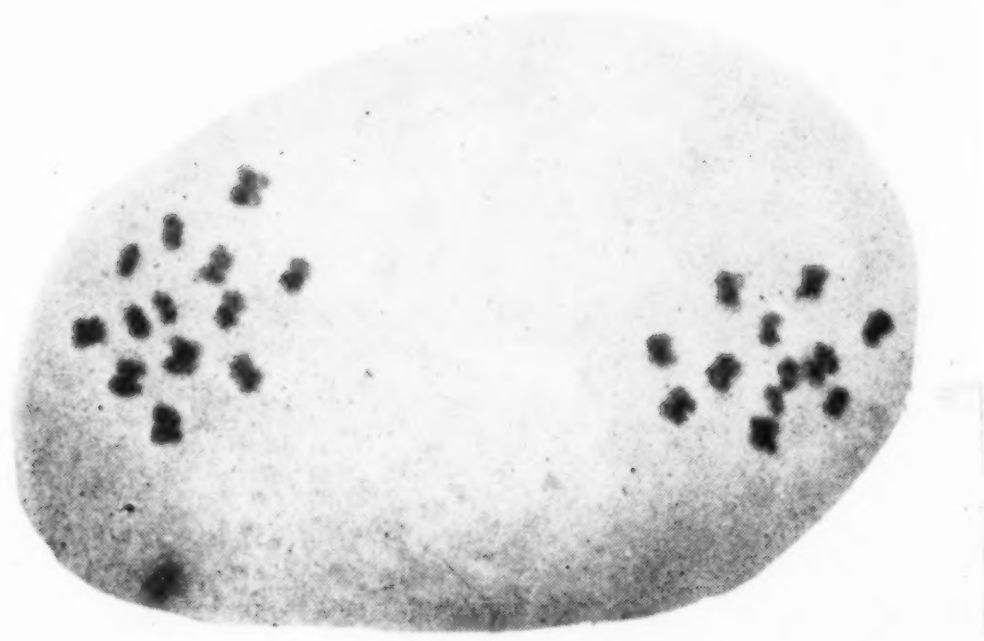
The eight bivalent chromosomes are of three sizes and twists and turns in the larger ones can also be made out. The lack of accommodation in the camera, makes it impossible to obtain the depth of focus that the human eye affords, even without the use of the focusing screw.

somes in pollen-mother-cells, and sometimes even in root-tips, may not show perfect fixation. (By perfect fixation is meant such fixation as has been attained in smear preparations of grasshopper spermatocytes, for instance.) But preparations of pollen-mother-cells in iron-acetocarmine allow of instantaneous and perfect fixation, and also of the cytoplasm being squeezed out from the cell-wall into a flat plate adhering to the cover-glass (or to the slide). (N. A. Cobb seems the first to have suggested such squeezing out of the chromosomes, in regard to nematodes.) A flat cytoplasmic plate in which the chromosomes are in contact with the cover-glass is excellent for photograph-



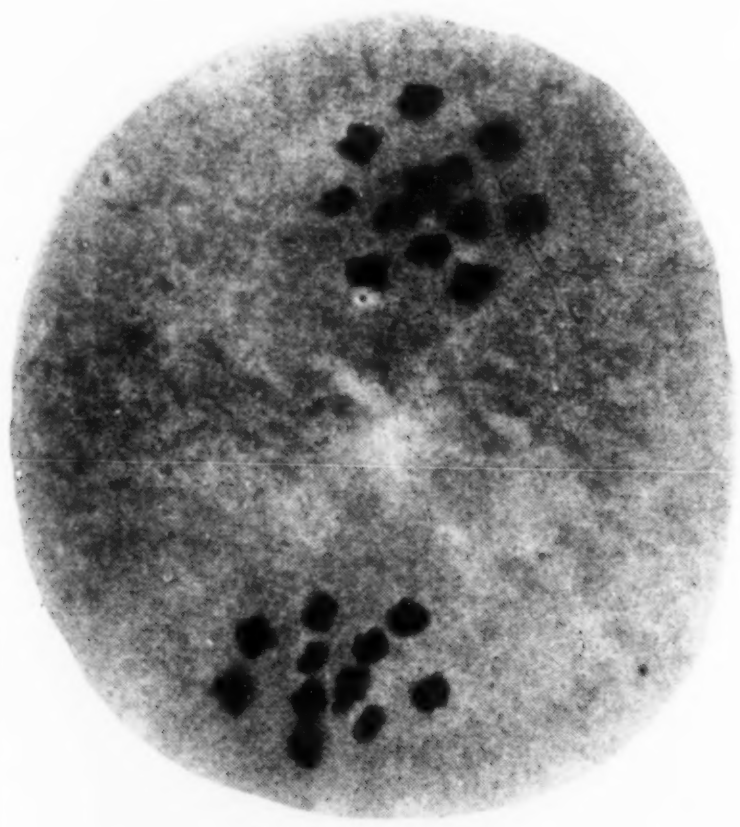
First metaphase of the haploid Datura.

Figure 12



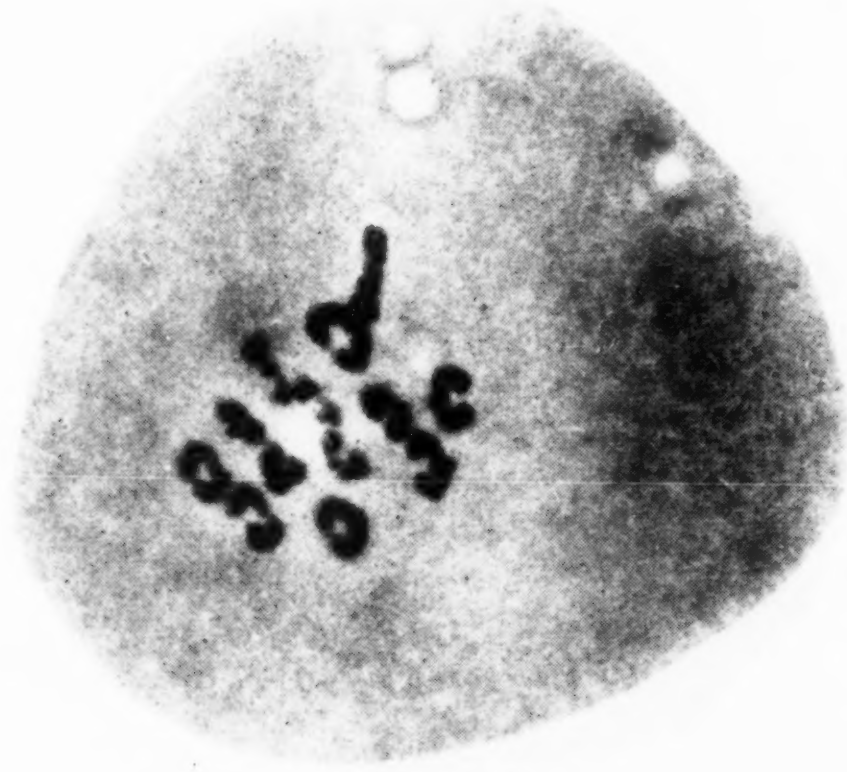
Four-lobed chromosomes at second metaphase of a 25-chromosome Datura mutant.

Figure 13



Four-lobed split chromosomes at second metaphase of a 23-chromosome Datura mutant.

Figure 14



Bivalents and trivalent of a $2n+1$ *Datura* mutant.

Figure 15

CHROMOSOMES OF DATURA

In datura a whole series of chromosomal mutations is known (see the Journal for May, 1927, pp. 193-199). These photographs show some of the abnormal chromosome arrangements that cause these chromosomal mutations. The haploid datura (Figure 12) has twelve instead of the usual 24 chromosomes. The 25 chromosome mutant *Hg* (Figure 13), has an extra chromosome in one of the pairs, making 13 in one group instead of 12. The chromosomes in Figure 14 are from a mutant branch, in which one of the chromosomes is lacking. Figure 15 shows an extra chromosome mutation, *Sg*, in which the extra chromosome is attached to one of the others, making a trivalent, of the ring and rod form.

ing with an oil-immersion objective. With specimens flattened on the slide itself, a water-immersion objective is better. It is, of course, one aim of photography with the microscope, that the pictures should show fine details not visible by looking through the eyepiece. This ideal has not yet been attained with ordinary light. However, photographs taken with the best optical arrangements, conforming to the laws of scientific microscopy, may be useful; even though they do not seem to show quite as much as can be seen by the eye through the microscope. For the accommodation of the lens of the eye adds depth, even if the focussing screw is not worked.

The six photographs here reproduced were taken with a correct optical apparatus. Of the two optically correct methods of photographing with an apochromatic objective, namely the projection eyepiece and the homal (amplifier), the latter was used. A well-corrected immersion condenser gave a large cone of light. The corrections were further improved by the use of a Wratten yellow-green light filter. Isochromatic non-halation plates were employed. Enlargements were made from the negatives.

Figure 10 represents the reduction metaphase in the well-investigated *Tradescantia virginiana*. There are twelve nearly equal bivalents, in the form of rings. As is well known, the chromomeres show particularly distinctly in this plant; and they are conspicuous in the photograph. The longitudinal split can be seen in places. (One or two of the bivalents have been broken by the pressure which was applied.)

Figure 11 is a photograph of the first metaphase in the diploid hyacinth, *H. orientalis*. The eight bivalents are clearly shown; four large, crossing over at one or two points; two medium; and two small ones, forming crosses.

Figure 12 depicts the reduction metaphase of the haploid Datura. The 12 univalents of different sizes are clearly visible.

Figure 13 shows the second-metaphase groups of the $2n + 1$ Datura mutant *Sg*. One group shows 13 and the other 12 chromosomes. The four-lobed form of the chromosomes is clearly visible.

Figure 14 shows the second-metaphase groups of a $2n$-1 mutated branch of Datura. One group has 12 and the other 11 chromosomes.

Figure 15 shows the first metaphase in the $2n + 1$ Datura mutant, *Hg*. There are eleven bivalents forming rings of different sizes, and one trivalent of the ring-and-rod form.

Figures 12 and 13 were taken with the apochromatic water-immersion of 1.25 aperture. The other figures were taken with the apochromatic oil-immersion of 1.4 aperture. A condenser cone of about 1.1 to 1.2 true aperture was used. The Goldberg wedge was found useful to ascertain at once the correct exposure.

Biological Miracles

(*Continued from page* 370)

harm if one goes at it with care in the early stages of growth; or with proper technique, combination animals can be produced, "made up," from the individuals of two species. These miraculously engendered animals are remarkable no less for their origin than for the far-reaching deductions that follow from their development.

The book is recommended to all those whose enjoyment of things is enhanced by an understanding of how they are "put together."

J. H. K.